EL CANIBALISMO SEXUAL EN LA TARÁNTULA IBÉRICA (*Lycosa hispanica*): ECOLOGÍA Y EVOLUCIÓN DE ESTRATEGIAS CONDUCTUALES

TESIS DOCTORAL

Rubén Rabaneda Bueno

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Madrid, 2014

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DE INVESTIGACIONES
CIENTÍFICAS

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Este trabajo ha sido financiado por una beca pre-doctoral I3P-BPD2004-CSIC y el proyecto del Ciencia e Innovación/FEDER (CGL2004-03153)

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Memoria presentada por Rubén Rabaneda Bueno para optar al Grado de Doctor por la Universidad Autónoma de Madrid

El Doctorando

Rubén Rabaneda Bueno
Madrid, septiembre de 2014

El **Dr. Jordi Moya Laraño**, Científico Titular de la Estación Experimental de Zonas Áridas-CSIC y la **Dra. Carmen Fernández Montraveta**, Profesora Titular de la Universidad Autónoma de Madrid

CERTIFICAN

Que los trabajos de investigación realizados en la Memoria de Tesis Doctoral: "**El canibalismo sexual en la tarántula ibérica (*Lycosa hispanica*): Ecología y evolución de estrategias conductuales**", son aptos para ser presentados por el Ldo. Rubén Rabaneda Bueno ante el Tribunal que en su día se designe, para aspirar al Grado de Doctor en Ciencias Biológicas por la Universidad Autónoma de Madrid.

Y para que así conste, en cumplimiento de las disposiciones vigentes extendemos el presente certificado a 25 de agosto de 2014 en Almería y Madrid.

VºBº Director VºBº Directora

Dr. Jordi Moya Laraño **Dra. Carmen Fernández Montraveta**

A mis padres Juan José y María del Carmen,
a mis hermanos Juanjo, Raúl y Javier.

"El sexo es una trampa de la naturaleza para no extinguirse."

— Friedrich Nietzsche

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RESUMEN

ABSTRACT

Resumen

El canibalismo sexual es un comportamiento extremo en el que las hembras generalmente matan y se alimentan del macho antes, durante o tras el apareamiento, y puede imponer elevados costes reproductores sobre los machos y las hembras. El balance de costes y beneficios dependerá del momento del canibalismo respecto a la cópula, y tendrá la máxima implicación si los individuos que participan en la interacción caníbal aún no se han apareado ya que, si la hembra no encuentra más machos, ninguno de los dos individuos podrá producir descendencia. El canibalismo sexual también puede afectar a la eficacia biológica de las hembras caníbales ya apareadas, cuando la poliandria (la hembra se empareja con más de un macho) contribuye a que la descendencia tenga mayor viabilidad. Sin embargo, si la hembra obtiene un beneficio alimentario y puede conseguir machos adicionales para aparearse, el canibalismo sexual se convierte en un conflicto de intereses extremo, dado que la hembra puede querer canibalizar al macho, mientras que está en el interés de éste último conseguir escapar para copular con otras hembras,

Este fuerte conflicto ha hecho que los investigadores se pregunten por el origen evolutivo del canibalismo sexual pre-cópula y su mantenimiento en las poblaciones naturales. Ello ha originado recientemente la interpretación del canibalismo sexual como un síndrome comportamental, en que las hembras vírgenes matarían al macho no por necesidades nutricionales, sino porque las hembras más agresivas pueden haber sido seleccionadas por el hecho de que una mayor agresividad (o voracidad) lleva a una mayor tasa de crecimiento y fecundidad, y al ataque indiscriminado a los machos por un simple lastre (o salpicadura) genético/a. Contrasta con esta idea el hecho de que se comprueba frecuentemente que las hembras de especies caníbales no atacan a los machos hasta que se han asegurado el esperma o sólo si la escasez de alimento es considerable.

En la presente tesis se aportó información para responder a algunos de estos interrogantes, utilizando como organismo modelo de estudio a la tarántula

ibérica (*Lycosa hispanica*), una especie en la que el dimorfismo sexual en el tamaño es relativamente bajo, lo que convierte a los machos en presas de muy gran tamaño relativamente al resto de presas naturales.

En el manuscrito I se contrasta experimentalmente la relación entre el consumo de un macho y la eficacia biológica de las hembras a través de diversas estimas de éxito reproductor. Asimismo, se pretende conocer si el canibalismo sexual es un comportamiento frecuente en la naturaleza y si depende de la disponibilidad de machos. Los resultados de este estudio muestran que el consumo experimentalmente inducido de un macho incrementa significativamente la fecundidad de las hembras respecto a las hembras que no se alimentan de un macho, que el canibalismo sexual tiende a ocurrir una vez las hembras se han apareado y que una mayor disponibilidad de machos aumenta las tasas de canibalismo sexual. A pesar de que el canibalismo parece un comportamiento principalmente adaptativo en una gran proporción de hembras, en algunos casos implicó la falta de fecundación de los huevos,, ya que algunas hembras caníbales que atacaron a los machos siendo vírgenes no consiguieron producir un saco de huevos, lo que sugiere la presencia de hembras agresivas que atacan a los machos por lastre genético.

En el manuscrito II se estudió la relación entre los niveles de voracidad alimenticia de las hembras y su tendencia al canibalismo sexual pre-cópula (lastre genético). Los resultados de este estudio ponen de manifiesto que cuanto mayor es la voracidad de las hembras antes de aparearse por primera vez, mayor es la probabilidad de que ataquen a los machos siendo vírgenes. Además, se comprobó que estas hembras más agresivas no discernían entre los fenotipos de los machos que mataban, mientras que las hembras vírgenes menos voraces (sin evidencia de lastre genético agresivo), mataron a los machos antes de copular sólo si éstos tenían una baja condición corporal.

En el manuscrito III se contrasta la hipótesis de diversificación de la poliandria según la cual la descendencia de madres poliándricas es fenotípica y genotípicamente más variable que la descendencia de madres monándricas (se aparean con un único macho), lo que podría servir para contrarrestar la estocasticidad ambiental favoreciendo la supervivencia de al menos una

proporción de la descendencia frente a cambios impredecibles en el ambiente (hipótesis del reparto de apuestas o "bet-hedging"). Con tal fin, se analizaron los datos de una serie de experimentos de campo y laboratorio en dos años consecutivos en los que las hembras tenían distintos niveles de acceso a los machos. Los resultados muestran que la poliandria promueve la variabilidad de tamaños y tasas de crecimientos de la descendencia pero, en contra de las predicciones de la hipótesis del reparto de apuestas, la eficacia biológica de las madres poliándricas (estimada a partir de la media geométrica del crecimiento y supervivencia de las crías en dos ambientes de laboratorio en los que se manipuló la disponibilidad de alimento) no fue significativamente superior a la de las madres monándricas.

En el manuscrito IV, mediante simulaciones basadas en los individuos, se determina si dos estrategias conductuales distintas, lastre agresivo y docilidad plástica, pueden coexistir en la naturaleza. Los resultados de este estudio muestran que una estrategia de lastre agresivo alternativa en la que la mayor agresividad fuera asociada con la maduración temprana, y en la que se atacan a los machos indiscriminadamente, puede coexistir con otra en que las hembras esperen a conseguir esperma antes de atacar a los siguientes machos que las visiten (docilidad plástica). Los análisis de datos de campo muestran que, efectivamente, estas dos estrategias se dan en una población natural de *L. hispanica,* en la que la estrategia más dócil presenta un rasgo sorprendente, ya que las hembras permanecen sin alimentarse hasta que consiguen copular con un macho, cambiando bruscamente tras la primera cópula a una alta tasa de forrajeo, superior a la de las hembras con agresividad por lastre genético. Estos resultados pueden contribuir a una compresión de la evolución de las personalidades animales y a explicar la presencia de polimorfismos conductuales dentro de las poblaciones.

Abstract

Sexual cannibalism is an extreme sexual conflict in which females kill and feed on males before, during or after mating. This behavior may be costly to both sexes and the net balance between the costs and benefits of sexual cannibalism depends on the timing of occurrence with regards to mating, being more relevant when none of the partners has previously mated. For the female this is more so if she has a low expected chance of finding additional males. Sexual cannibalism can also undermine female reproductive success if polyandry (female mating with multiple males) enhances offspring viability. However, when females accrue feeding benefits from killing males and have future mating expectations with other males, sexual cannibalism becomes an extreme sexual conflict, since females may be prone to sexual cannibalism while males should attempt to escape female attacks to search for, and mate with other females, especially if the male fails to do so with the cannibalistic female.

This strong conflict have puzzled researchers for one century and a half, who wonder about the evolutionary origin of sexual cannibalism and its maintenance in natural populations. Recently, a new interpretation has been put forward which sees sexual cannibalism as a behavioral syndrome by which virgin females attack males not because the potential nutritional benefits, but because high aggressiveness (or voraciousness) is likely favored by natural selection in a context other than sexual, as it contributes to increase growth rates and fecundity. This then leads aggressiveness to genetically spill over into indiscriminate attacks on males. This contrasts with the evidence that females of cannibalistic species tend to attack males only when the former have achieved the sperm necessary to fertilize their eggs following mating with other males, and also runs contrary to the prediction by a published model that a female will attack males only if she is food limited.

The present PhD thesis contributes to answer some of these questions by using the Iberian tarantula (*Lycosa hispanica*) as a model organism. Sexual size

dimorphism in this species is relatively low, and males are therefore relatively very large prey items as compared to natural prey.

In the manuscript I, the relationship between the consumption of a male and female fitness was experimentally tested using several estimates of female reproductive success. Additionally, the present work served to reveal whether sexual cannibalism is a common behavior in nature and to experimentally test whether it depends on male availability. The results of this study show first, that the experimentally-induced consumption of a male significantly increases female reproductive success relative to females not feeding on a male. Second, that sexual cannibalism is more likely to occur once females have mated with a male, and third that the rates of sexual cannibalism increase with male availability. Despite the fact that sexual cannibalism seems to be an adaptive strategy for most females, in some cases it was associated with the lack of egg fertilization, as some cannibalistic females that attacked males when the former were still virgin were unable to produce an egg sac, suggesting that spillover aggression is present in some females and that they indiscriminately attack males.

In manuscript II, I investigated the relationship between the levels of female feeding voraciousness and her tendency towards pre-copulatory sexual cannibalism (spillover). The results of this study show that the probability that a virgin female attacks an approaching male increases with her voracity prior to her first mating. In addition, I demonstrated for the first time that highly aggressive females (consistent with an spillover behavioral syndrome) did not discriminate among the phenotypes of the males they killed, whereas virgin females of low voracity killed males before mating only if males had relatively poor condition.

In manuscript III, I tested the diversifying hypothesis of polyandry, according to which the offspring of polyandrous mothers are genetically (and thus phenotypically) more variable than the offspring of monandrous mothers (i.e., those mating with a single male), which could serve to cope with environmental stochasticity by favoring the survival probability of at least some offspring when the environment changes unpredictably (bet-hedging hypothesis). To this end, I analyzed field and laboratory data from two consecutive years of experiments in which females had differential access to males. The results of this study show that

polyandry affects positively the variability in offspring size and growth rates, but contrary to the predictions of the bet-hedging hypothesis, the reproductive fitness of polyandrous mothers (i.e. estimated though the geometric mean fitness of spiderlings growth and survival across two feeding laboratory environments varying in prey quantity) was not significantly higher than that of monandrous mothers.

In manuscript IV, we develop individual based models aimed to unveil whether two genetically-based behavioral types, aggressive spillover and plastically docile, can coexist in natural populations. The results of this study show that an alternative aggressive spillover strategy in which high aggressiveness leads to early maturation and to indiscriminate attacks to males can coexist with a strategy in which females first mate to grant sperm and subsequently attack the additional males visiting them. Analyses of field data show that both strategies can be present in a natural population of *L. hispanica*, and it is particularly intriguing the fact that females showing the docile strategy will not feed until they have achieved their first copulation with a male, at which moment turn into highly voracious, even more so than spillover females. These results contribute to our understanding about the evolution of animal personalities and to explaining the presence of behavioral polymorphisms in animal populations.

INTRODUCCIÓN GENERAL

Introducción

I. EL CANIBALISMO SEXUAL: UN CONFLICTO SEXUAL EXTREMO

El canibalismo sexual, el ataque y consumo de una potencial pareja reproductora dentro de un contexto sexual, es un comportamiento casi exclusivo de artrópodos y particularmente extendido en las arañas, en el que la hembra suele atacar al macho antes, durante o inmediatamente después de la cópula (Elgar, 1992). El canibalismo sexual es un fenómeno taxonómicamente raro, que aparece sólo en invertebrados, y con mayor frecuencia entre varios grupos de insectos y arácnidos, destacando su prevalencia en arañas, escorpiones y mántidos (Elgar, 1992; Polis, 1981). Se ha sugerido que el canibalismo sexual ha evolucionado de forma independiente varias veces, manteniéndose a través de diferentes fuerzas selectivas (Elgar, 1992; Morse 2004).

El conflicto sexual se origina debido a que los sexos tienen diferentes óptimos de eficacia biológica para un mismo rasgo, como por ejemplo la frecuencia de cópula (Anrqvist & Rowe, 2005). En este sentido, el estudio del canibalismo sexual se revela importante desde un punto de vista ecológico y evolutivo, ya que es una forma extrema de conflicto sexual (Schneider & Lubin, 1998), y como tal podría tener una gran influencia en los procesos de selección sexual (Andersson, 1994; Chapman et al., 2003). Debido a esto, el canibalismo sexual ofrece una oportunidad única para identificar con exactitud los costes y beneficios del conflicto sexual para machos y hembras, de determinar si el canibalismo es un comportamiento adaptativo y evolutivamente estable tanto para el macho como para la hembra, y de identificar la existencia de coevolución antagonista (Parker, 1979; Rowe et al., 1994; revisado en Arnqvist & Rowe, 2005). De hecho, el canibalismo sexual tiene un gran potencial como agente selectivo de diversos caracteres morfológicos y conductuales, incluso cuando es un comportamiento poco frecuente (Morse, 2004), debido a que su impacto sobre la eficacia biológica de los individuos es inmediato (Persons & Uetz, 2005) y contribuye a generar patrones de fertilidad y viabilidad sobre los que puede intervenir la selección natural (Darwin, 1859, 1871; Endler, 1986).

II. VALOR ADAPTATIVO DEL CANIBALISMO SEXUAL. IMPLICACIONES ECOLÓGICAS Y EVOLUTIVAS

El canibalismo sexual ha centrado el interés de los biólogos evolutivos desde que Darwin introdujera el concepto de selección sexual (Darwin, 1871). Desde entonces, se ha debatido mucho sobre el valor adaptativo del canibalismo sexual, y la controversia sobre su significado funcional y adaptativo (Johns & Maxwell, 1997) acapara gran parte de la investigación que busca entender su origen, evolución y mantenimiento en la naturaleza (Thornhill, 1976; Elgar, 1992; Elgar & Schneider, 2004). Aunque se ha sugerido que el canibalismo sexual es un comportamiento demasiado raro para ser considerado significativo (Gould, 1984), lo cierto es que a día de hoy existen pruebas que indican que puede ser una estrategia o comportamiento adaptativo que puede influir en los procesos de selección natural y selección sexual sobre los rasgos de machos y hembras. Parece, por tanto, que el canibalismo sexual no es un incidente meramente anecdótico o casual, sino más bien el resultado de un complejo proceso evolutivo en el que intervienen los intereses reproductores de ambos sexos (Bateman, 1948; Trivers, 1972). El valor adaptativo del canibalismo sexual dependerá del balance de costes y beneficios que afecten a machos y hembras, que influirá de forma diferente sobre la eficacia biológica individual dependiendo de las características fenológicas de la especie; es decir, de cómo se solapen las abundancias de machos y hembras en el tiempo y la de la variabilidad ambiental (Elgar, 1992; Elgar & Schneider, 2004; revisado en Wilder et al., 2009). Estos costes y beneficios tienen la forma de fuertes presiones selectivas que condicionan la frecuencia y ocurrencia de los ataques de las hembras e influyen en la evolución de adaptaciones que podrían explicar tanto la motivación de las hembras a capturar machos como la de los machos a escapar de esos ataques o su vulnerabilidad. La investigación del canibalismo sexual se ha centrado principalmente en los dos primeros aspectos, aunque el tercero (la evolución de la invulnerabilidad en los machos) podría ser igualmente importante para estimar con exactitud la frecuencia del canibalismo sexual en la naturaleza y entender la coevolución de los sexos (revisado en Wilder et al., 2009).

Un factor clave en el balance entre los costes y los beneficios del canibalismo sexual para ambos sexos es el momento en que se produce en relación a la transferencia espermática ("timing"), que puede ser antes (canibalismo sexual pre-copulatorio, *Pre-copulatory Sexual Cannibalism:* pre-SC, en inglés, de ahora en adelante), durante (dc-SC) o después (post-SC) (Elgar, 1992). En el macho, estos costes están asociados con una limitación de la capacidad de maximizar su eficacia biológica (éxito reproductor) a través del emparejamiento con múltiples hembras (Bateman, 1948), ya que el canibalismo implica una reducción de sus oportunidades de emparejamiento, sean los machos vírgenes o no (revisado en Elgar, 1992; Johns & Maxwell, 1997). Cuando los machos son vírgenes y el canibalismo sexual ocurre antes de la transferencia espermática, los costes tienden a acentuarse, debido a la imposibilidad de dejar descendencia (Elgar, 1992; Elgar & Fahey, 1996; Arnqvist & Henriksson, 1997). Sin embargo, las pérdidas de valor reproductivo para el macho, así como la intensidad del conflicto sexual, deberían disminuir cuando el canibalismo ocurre durante o después de la inseminación (Ej. Andrade, 1996). En la hembra, el margen de beneficios potenciales es mayor, pero el balance de costes y beneficios también dependerá del momento en que ocurra el canibalismo. Los costes tienden a disminuir cuando la hembra ataca al macho tras la transferencia de esperma a su espermateca. Cuando el canibalismo tiene lugar antes de la inseminación y la hembra es virgen, pone en riesgo la fertilización de sus huevos y, con ello, se arriesga a que su eficacia biológica sea nula. Otros factores relevantes que pueden determinar si el canibalismo sexual es o no adaptativo para el macho y/o para la hembra son las preferencias de pareja y el sistema de apareamiento de las hembras (monandria/poliandria), los comportamientos de evitación del canibalismo del macho y las características ambientales (disponibilidad de alimento y/o de pareja y presión de depredación) (Elgar, 1992; Johnson, 2003; Wilder et al., 2009).

Según el significado funcional del canibalismo sexual, tanto desde el punto de vista del macho como de la hembra, se pueden distinguir dos grupos principales de hipótesis (Elgar, 1992). Por un lado, las **hipótesis adaptativas** tienen en cuenta (1) las decisiones de forrajeo y el nivel de hambre de la hembra, o si ésta ya ha conseguido esperma copulando previamente con otro macho (Newman & Elgar,

1991), (2) la elección de pareja en función de los rasgos fenotípicos del macho (Elgar & Nash, 1988; Prenter et al. 2006) y (3) la inversión terminal paterna a través del sacrificio (complicidad) del macho (Andrade, 1996). Por otro lado, las **hipótesis no adaptativas** consideran el canibalismo sexual como un subproducto de la "personalidad" agresiva (síndrome conductual) de la hembra (Arnqvist & Henriksson, 1997), que podría llevar a que ésta confunda al macho con una de sus presas ("hipótesis de la identidad equivocada", Gould, 1984) o, sencillamente, le ataque indiscriminadamente a pesar de reconocerlo. La hipótesis del sacrificio del macho sirve para explicar el canibalismo sexual que se produce durante o después de la inseminación; las hipótesis del forrajeo adaptativo, elección de pareja y síndrome agresivo sirven para explicar el canibalismo sexual antes de la cópula. Estas hipótesis no son mutuamente excluyentes, y pueden complementarse para explicar la evolución y mantenimiento del canibalismo sexual entre especies y dentro de cada especie. Por ejemplo, en la araña de "espalda" roja *Latrodectus hasselti* (Theridiidae) el "sacrificio" del macho en el apareamiento proporciona a éste una ventaja de paternidad (Andrade, 1996), pero el éxito reproductor final del macho, así como la probabilidad de ser canibalizado es fuertemente dependiente del estado nutricional de las hembras (Andrade, 1998). Cabe destacar, sin embargo, que una antigua hipótesis, la del suicidio del macho tras la cópula para alimentar a la propia descendencia (Buskirk et al., 1984) no presenta ningún tipo de apoyo hasta la fecha, y existe considerable consenso sobre su falta de plausibilidad (Elgar & Schneider, 2004).

De hecho, las teorías que mejor reflejan los costes y beneficios del canibalismo sexual son aquellas que predicen sus efectos antes de la cópula (pre-SC), ya que el canibalismo sexual por parte de hembras que no hayan copulado previamente implicaría una limitación de la capacidad de las hembras de fertilizar los huevos si acaban con los donantes y la densidad de machos es escasa (Buskirk et al., 1984; Elgar, 1992). En esta tesis, debido a las características de la especie modelo utilizada (prevalencia de pre-SC), me centraré solamente en las hipótesis adaptativas del forrajeo y la elección de pareja y en la hipótesis no adaptativa del síndrome por salpicadura agresiva.

III. HIPÓTESIS ADAPTATIVAS DEL CANIBALISMO SEXUAL PRE-CÓPULA

Hipótesis del forrajeo adaptativo

Según la hipótesis del forrajeo adaptativo (Newman & Elgar, 1991), el canibalismo sexual pre-cópula habría evolucionado porque incrementaría la fecundidad de las hembras y paliaría la limitación de alimento, que es bastante frecuente en las arañas (Wise, 1993). El modelo del forrajeo adaptativo tiene en cuenta el estado copulatorio y el nivel de hambre de las hembras, y explica por tanto el pre-SC en base a un compromiso ("trade-off", en inglés) entre el incremento de la fecundidad por canibalismo y la falta de reproducción por limitación espermática. Hay dos factores ecológicos que determinan si el canibalismo sexual es o no un comportamiento adaptativo de la hembra: la tasa de encuentros macho-hembra y el incremento de masa corporal (condición) como resultado del forrajeo de presas heteroespecíficas. El modelo del forrajeo adaptativo predice que las hembras se comportarán adaptativamente canibalizando machos cuando su nivel de hambre sea elevado (limitación de alimento) y una vez que se hayan apareado. El canibalismo sexual estará regulado por las necesidades inmediatas de la hembra de incrementar su fecundidad y fertilidad, de modo que la tendencia de la hembra a atacar a un macho dependerá del valor relativo de éste como fuente de esperma o alimento, y por tanto de la disponibilidad de machos y del acceso que tengan a los mismos. Una de las predicciones de la hipótesis del forrajeo adaptativo es que la prevalencia de pre-SC aumentará con la disponibilidad de machos (tasa de encuentros macho-hembra) y con la escasez de alimento (baja disponibilidad de presas), y disminuirá cuando los machos sean menos abundantes o menos móviles (menor disponibilidad/acceso a machos) y la disponibilidad de presas sea alta. Otra predicción es que las hembras caníbales deberían mejorar significativamente su fecundidad respecto a las que no lo son.

Los estudios de campo realizados con la tarántula ibérica (*Lycosa hispanica*, antes *L. tarantula*) (Lycosidae) sugieren que las hembras pueden sufrir limitación por alimento en la naturaleza (Moya-Laraño, 1999, 2002a; Moya-Laraño et al., 2003b) y podrían apoyar esta hipótesis (Moya-Laraño et al., 2003a,b). Además, la condición corporal de la hembra antes de depositar la puesta tiene un efecto

importante sobre su eficacia biológica (número de crías, peso de la puesta, etc.) (Moya-Laraño, 2002), que podría ser favorecida si el consumo de machos incrementara la condición corporal. En esta araña, las hembras pequeñas de maduración tardía que tienen mejor condición corporal y aún no se han apareado parecen ser menos agresivas y tienen un mayor éxito en las cópulas que las hembras de maduración tardía de mayor tamaño y en peor condición corporal, llegando las arañas más tardías a tener un escaso acceso a los machos, lo que sugiere que el sexo masculino es un recurso limitante para las hembras (Moya-Laraño et al., 2003a). Esto significa que las hembras podrían responder adaptativamente en función de la disponibilidad de machos, al ser ésta baja al final de la estación reproductora (Moya-Laraño et al., 2003a,b). La limitación espermática puede deberse en parte al canibalismo de las hembras de maduración temprana, por lo que habría competencia por el acceso a los machos como fuente de esperma y alimento. Una vez que las hembras de maduración tardía se han apareado, éstas podrían volverse más agresivas, aumentando su tendencia al canibalismo (Johnson, 2001; Herberstein et al., 2002). El hecho de que estas arañas defiendan territorios de forma altamente agresiva, llegando al canibalismo entre hembras (Moya-Laraño et al., 2002), apoyaría esta idea.

La hipótesis del forrajeo adaptativo encuentra cierto apoyo en algunos ejemplos de canibalismo en anfípodos (Dick, 1995) y mántidos (Barry et al., 2008), en los que parece haber beneficios nutricionales. En arañas aún no se ha determinado con exactitud que las hembras obtengan beneficios de este tipo, ya que los pocos estudios que han puesto a prueba esta hipótesis se han realizado en condiciones de laboratorio (Elgar, 1992; Arnqvist & Henriksson, 1997; Johnson, 2001; Schneider & Elgar, 2002; Wilder & Rypstra, 2008), y hay escasa evidencia de que en la naturaleza las hembras ataquen a los machos en función de su nivel de hambre (Andrade, 1998; Schneider & Elgar, 2001; Herberstein et al., 2002; Persons & Uetz, 2005, Wilder & Rypstra, 2008; Berning et al., 2012). De hecho, son varios los estudios que no han encontrado relación entre la historia alimenticia de la hembra y su tendencia al canibalismo antes de la cópula (Jackson, 1980; Arnqvist & Henriksson, 1997; Spence et al., 1996; Fromhage et al., 2003; Johnson, 2005). Por otra parte, pocos estudios que hayan examinado los efectos del consumo de un macho han encontrado efectos positivos sobre la fecundidad de la hembra (Ej:

Birkhead et al. 1988). Por ejemplo, en la araña pescadora europea (*Dolomedes fimbriatus*) (Pisauridae) los niveles de limitación de esperma y alimento no explican la tendencia de la hembra a atacar a un macho, ya que la historia de forrajeo (depredación y canibalismo sexual) y la fecundidad no están correlacionados (Arnqvist & Henrikkson, 1997). En dos estudios recientes con la araña *Agelenopsis penlsylvanica* (Agelenidae) el canibalismo sexual pre-cópula incrementó las posibilidades de producir un saco de huevos y su éxito de eclosión una vez formado, aunque no influyó en otros parámetros de la fecundidad, tales como el peso de la puesta o el número de huevos producidos (Berning et al., 2012; Pruitt et al., 2014). En otros tres estudios con arañas, se ha mostrado que el consumo de machos mejora significativamente la fecundidad de la hembra al incrementar la densidad energética de los huevos (Blamires, 2011) y la supervivencia de las arañitas (Welke & Schneider, 2012; Wu et al., 2013).

Por otra parte, se sabe que las arañas pueden alimentarse selectivamente de diferentes presas según sus necesidades nutricionales (Greenstone, 1979; Mayntz et al., 2005), y que esto será determinante para su fecundidad, supervivencia y crecimiento (Uetz, 1992; Mayntz & Toftz, 2001; Wilder & Rypstra, 2008). Esto podría tener importantes implicaciones para el canibalismo sexual, porque los machos de algunas especies pueden tener nutrientes y aminoácidos esenciales en proporciones similares o muy próximas a las requeridas por las hembras, en comparación con la composición nutricional de otras presas (Denno & Fagan, 2003). Por ejemplo, se puede anticipar que el canibalismo sexual podría proporcionar aminoácidos esenciales que intervienen en la producción de seda, que se se ha visto que son determinantes en la eficacia biológica de las hembras (Craig et al., 2000). En este sentido, aunque la abundancia de presas sea alta, los machos podrían ser una presa especialmente valiosa para paliar la limitación de ciertos nutrientes carentes en la dieta de las hembras (Samu, 1993; Mayntz & Toft, 2006).

Hipótesis de la elección de pareja

Otra explicación que se ha dado del canibalismo sexual pre-cópula es la hipótesis de la elección de pareja (Elgar, 1992; Elgar & Nash, 1988; revisado en Prenter et al., 2006), que tiene en cuenta la variabilidad fenotípica de los machos asociada a diferencias en su éxito reproductor, y en base a la cual las hembras elegirían a los machos de mayor calidad como pareja, desechando a los machos con peores fenotipos a través del canibalismo. Una consecuencia del canibalismo selectivo de machos puede ser la desviación positiva hacia los fenotipos de mayor calidad (Halliday, 1983; Maynard Smith, 1987) que, al interferir con la proporción poblacional de sexos ("sex ratio"), podría promover variación en la frecuencia de los rasgos del macho y de la hembra, que a su vez determinan la frecuencia de canibalismo sexual (Vollrath & Parker, 1992; Prenter et al., 2006). Para entender el canibalismo sexual como una forma de elección de pareja habría que considerar distintos aspectos de las historias de vida de las hembras, tales como el riesgo de depredación y/o su historia alimentaria reciente (Crowley et al., 1991; Sih, 1994), que podrían condicionar sus decisiones de emparejamiento (Rowe et al., 1994). Por ejemplo, el modelo verbal de Prenter et al. (2006) predice que las hembras deberían poder modificar su comportamiento caníbal de acuerdo a la tasa de encuentros y la disponibilidad de machos, por lo que esta estrategia podría entenderse mejor en combinación con el forrajeo adaptativo. El canibalismo sexual podría mantenerse a partir de beneficios nutricionales (Newman & Elgar, 1991), a la vez que impondría selección direccional sobre caracteres morfológicos y conductuales del macho (Persons & Uetz, 2005).

Un rasgo del macho potencialmente seleccionable, el tamaño corporal absoluto del macho o el relativo a la hembra (dimorfismo sexual de tamaño, *Sexual Size Dimorphism, SSD*, en inglés), puede influir en la motivación de la hembra a atacar a un macho, o en la vulnerabilidad del macho tras ser atacado y, por tanto, en las tasas de canibalismo sexual (Elgar & Nash, 1988; Persons & Uetz, 2005; Wilder & Rypstra, 2008; Fernández-Montraveta et al., 2014). Sin embargo, más que un mecanismo directo de elección activa de pareja, la selección diferencial de machos podría ser una consecuencia indirecta del canibalismo de los machos más pequeños o en peor condición. Aunque no es posible distinguir si una hembra mata

a un macho de un determinado fenotipo por pura decisión de forrajeo o porque lo esté descartando como pareja, dado que ambas cosas ocurren en el mismo instante, un macho pequeño (o en baja condición), que suponga menos alimento para la hembra y a la vez tenga menos éxito reproductor y que sea canibalizado por una hembra sugeriría de forma muy importante que se trata de una forma directa de elección de pareja, dado que se trataría de machos menos provechosos como alimento. Sería de esperar que esto ocurriera también cuando las hembras tienen preferencias de emparejamiento según otros rasgos del macho, que determinen su elección como pareja en vez de como alimento. Por ejemplo, las hembras pueden moldear sus preferencias por los machos cuando son sub-adultas y según su exposición a éstos, haciendo que los fenotipos y estrategias de emparejamiento del macho sean determinantes en la tendencia caníbal de las hembras ya maduras (Hebets, 2003).

Algunos estudios sugieren que las hembras de arañas pueden tener preferencias de emparejamiento por determinados machos (Elgar et al., 2000; Hebets, 2003; Persons & Uetz, 2005; Schneider & Lesmono, 2008; Wignall & Herberstein, 2013), que pueden estar relacionadas con la agresividad (Pruitt & Riechert, 2009a; ver también Persons & Uetz, 2005) y/o tendencia al canibalismo de éstas (Hebets, 2003; Johnson, 2005). Además, el éxito de emparejamiento y la eficacia biológica de los machos podría depender de ciertas características morfológicas o conductuales de éstos, e implicaría que las hembras que eligen a los mejores machos para aparearse obtendrán beneficios indirectos al transferir sus genes a la progenie (Zahavi, 1975; Andersson, 1994; Jennions & Petrie, 2000; Simmons, 2005). Aunque pocos estudios empíricos han demostrado beneficios del canibalismo sexual sobre la eficacia biológica derivados de la elección de pareja de la hembra (Kokko et al., 2003), la mayoría de ellos han proporcionado apoyo parcial a esta hipótesis (Simmons, 1987; Alatalo et al., 1998; Moya-laraño & Fox, 2006; García-González & Simmons, 2007). Esto también es plausible en *L. hispanica*, donde las franjas negras abdominales de los individuos jóvenes están correlacionadas con la condición corporal (Moya-Laraño et al., 2003c). Si en los machos existe un patrón similar y las hembras adultas son capaces de utilizar estas

manchas para evaluar la condición corporal de éstos, podrían utilizar el canibalismo para descartar a los machos en peor condición corporal.

En algunos de los estudios que han examinado la relación entre el comportamiento agresivo de las hembras y el fenotipo de los machos se ha demostrado que ambos eran independientes (Ej: Elgar & Nash, 1988; Arnqvist & Henrikkson, 1997; Berning et al., 2012; ver abajo), y en otros se ha encontrado que las hembras canibalizaban al macho según su tamaño (Persons & Uetz, 2005; Wilder & Rypstra, 2008; Stoltz et al., 2008, 2009), o en función de rasgos conductuales asociados al cortejo y la cópula que podrían depender del tamaño y/o la condición corporal del macho (Stoltz et al., 2008, 2009; Wignall & Herberstein, 2013; ver también Schneider & Lesmono, 2009).

IV. HIPÓTESIS NO ADAPTATIVAS DEL CANIBALISMO SEXUAL PRE-CÓPULA

La hipótesis no adaptativa del **síndrome de agresión o personalidad por salpicadura agresiva** (*Agressive Spillover Hypothesis, ASH*, en inglés) propuesta por Arnqvist & Henriksson (1997) es una explicación alternativa al forrajeo adaptativo que surge a raíz de los resultados de sus experimentos en la araña pescadora europea *Dolomedes fimbriatus*, en la que los altos niveles de pre-SC indiscriminado tendrían consecuencias negativas sobre la eficacia biológica de las hembras (falta de fecundación de los huevos). Esta hipótesis sugiere que el pre-SC es un producto colateral de la agresividad de las hembras juveniles en el contexto de forrajeo, donde los altos niveles de voracidad hacia presas son adaptativos puesto que favorecen el crecimiento y tamaño final de la hembra, asociado a una fecundidad superior, que se sigue expresando cuando maduran a adultas y se manifiesta con el ataque indiscriminado a machos en el contexto sexual. Este síndrome de agresividad general puede atender, por tanto, a la presencia de rasgos conductuales en diferentes contextos ecológicos y momentos de la historia vital de las hembras, que terminarán influyendo en su eficacia biológica. La correlación en la agresividad entre los contextos juvenil (forrajeo) y adulto (emparejamiento) podría tener su origen en restricciones genéticas asociadas a la falta de flexibilidad conductual, que impedirían a las hembras ajustar su respuesta agresiva ante la presencia de machos. Hay varios factores que pueden ser importantes en dichas

restricciones. Por ejemplo, en arañas, las hembras adultas que han tenido experiencia con machos siendo inmaduras pueden mostrar tendencias caníbales definidas (Hebets, 2003; Johnson, 2005). En este caso, la experiencia temprana es una forma de consolidar el comportamiento agresivo de la hembra cuando madura, dando como resultado una disminución de la reversibilidad de sus respuestas conductuales en el contexto sexual. El papel de los machos en las interacciones caníbales también es importante, ya que puede condicionar el grado en que estas correlaciones afectan a la eficacia biológica de la hembra. Por ejemplo, los machos que son capaces de detectar a las hembras más agresivas (Robinson, 1982; Elgar, 1992; Moya-Laraño et al., 2003a) evitarán copular con ellas, y posiblemente se aparearán con las hembras más dóciles (Pruitt & Riechert, 2009a), lo que afectará negativamente a las posibilidades reproductoras de las hembras agresivas (ver también Pruitt & Riechert, 2009b). Sin embargo, éstas podrían atacar y consumir preferentemente machos grandes, nutricionalmente más provechosos, incrementando así su éxito reproductor respecto a las hembras dóciles (Pruitt et al., 2011), pero sólo si se pueden obviar los efectos genéticos indirectos de aparearse con machos de mayor tamaño.

Las correlaciones entre comportamientos a través de contextos o síndromes conductuales son frecuentes en el Reino animal, apareciendo en contextos muy diversos (Sih et al., 2004), y pueden afectar a rasgos fisiológicos o morfológicos que serían fijados debido a la expresión de comportamientos tempranos. Ya que las hembras actúan como depredadoras potenciales de los machos, el síndrome de agresividad en las interacciones de canibalismo sexual puede ser visto como un síndrome de agresividad general, equiparable a las correlaciones conductuales agresivas en las interacciones depredador-presa que implican a diversos rasgos relacionados con las habilidades de caza, el comportamiento antidepredador o la defensa territorial. Por ejemplo, en la araña *Agenelopsis aperta* (Agelenidae), los individuos más agresivos atacan rápidamente a presas o conespecíficos que invaden su territorio (Riechert & Hedrick, 1993), aunque no hay canibalismo involucrado (Maupin & Riechert, 2001). Hay varios rasgos que se correlacionan con la eficacia biológica de estas arañas, tales como el comportamiento de forrajeo (Hedrick & Riechert, 1989), el de lucha y defensa territorial (Maynard Smith &

Riechert, 1984; Riechert & Maynard Smith, 1989), y el comportamiento anti-depredador (Riechert & Hedrick, 1990), que se asocian con dos respuestas conductuales opuestas: agresión y miedo (Maynard Smith & Riechert, 1984). En poblaciones donde la disponibilidad de presas y de sitios para construir la tela son limitantes y hay pocos depredadores, la competencia territorial entre las arañas es muy alta, y las arañas responden rápidamente tanto dirigiéndose a una presa que cae en la tela (respuesta agresiva) como buscando refugio si detectan una amenaza potencial (respuesta miedo) (Hedrick & Riechert, 1989; Riechert & Hedrick, 1990). Sin embargo, en las poblaciones donde los recursos son abundantes y la presión de depredación es mayor, estas respuestas tienden a relajarse, de modo que las diferencias ecotípicas entre las poblaciones se acentúan (Hedrick & Riechert, 1991). Las diferencias ecotípicas en el comportamiento de forrajeo (Hedrick & Riechert, 1989) y depredador (Hedrick & Riechert, 1991) no se deben al nivel de hambre, experiencia o efectos maternos, sino a diferencias genéticas en la latencia (velocidad de reacción) a atacar presas, que además pueden reflejar diferencias en otros comportamientos como el antidepredador (Hedrick & Riechert, 1990). Este ejemplo muestra cómo los síndromes conductuales pueden evolucionar de manera divergente en distintas poblaciones. Esto significa que, si excluimos el contexto sexual y con ello eliminamos al canibalismo sexual de la ecuación de un conjunto de comportamientos correlacionados cuyo denominador común es la agresividad, el síndrome agresivo seguirá existiendo, ya que los demás rasgos correlacionados influirán sobre la eficacia biológica del individuo, y lo harán de forma diferente según el contexto donde se exprese ese rasgo. Dicho de otro modo, en las arañas el síndrome de agresividad puede involucrar a las relaciones macho-hembra, pero puede existir independientemente de éstas en otros contextos donde las relaciones sean del tipo depredador-presa. Los síndromes de agresividad pueden por tanto originar "trade-offs" como resultado de las presiones entre los contextos (p. ej: forrajeo, antidepredador), puesto que los distintos comportamientos están correlacionados. El canibalismo sexual como síndrome conductual no sería pues nada más que otra expresión conductual de síndromes ya establecidos, probablemente por presiones de selección que nada tienen que ver con el contexto sexual.

Los individuos con un tipo conductual (la configuración particular de comportamientos que expresan) agresivo serán más competitivos en situaciones donde sean favorables ciertos niveles de agresividad, pero dicha agresividad será contraproducente en situaciones donde ser cautelosos o menos agresivos sea más apropiado, como en los contextos de cuidado parental o antidepredador. Por el contrario, los individuos poco agresivos serán favorecidos en situaciones donde una baja agresividad sea óptima, pero estarán en desventaja respecto a los individuos más agresivos en situaciones competitivas. Igualmente, la voracidad de una hembra caníbal hacia sus presas implica un mayor éxito de forrajeo, que conducirá a un mayor tamaño y condición corporal y, como resultado, a una mejora de su fecundidad, pero puede llevar a que esta hembra mate al único macho que la visite e incurra en la no fecundación de sus huevos. La selección en conjunto del rasgo agresivo-voraz debido a la consistencia entre contextos arrastraría evolutivamente a comportamientos óptimos y sub-óptimos, favoreciendo la persistencia de estos últimos en la población. Este mecanismo evolutivo podría explicar la existencia de polimorfismos o continuos de personalidad de las hembras en diferentes poblaciones de arañas (Riechert & Maynard Smith, 1989; Pruitt et al., 2008; Fogarty et al., 2011; Kralj-Fišer & Schneider, 2012).

En un síndrome de agresividad, las restricciones impuestas por las correlaciones entre contextos o rasgos pueden superarse mediante cierto grado de plasticidad conductual, que permita a los individuos responder al entorno cuando el contexto cambia (Dingemanse et al., 2009). Por ejemplo, en *A. penlsylvanica* (Agelenidae) la tendencia al canibalismo no sólo depende de la agresividad general de la hembra (voracidad hacia presas), sino también de su nivel de hambre o estado alimenticio (forrajeo adaptativo) (Berning et al., 2012), entendiéndose mejor como una combinación de estrategias (Berning et al., 2012; Foellmer & Khadka, 2013). De forma similar, las hembras de algunas arañas ajustan sus niveles de agresión hacia los machos según su nivel de hambre (Andrade, 1998; Moya-Laraño et al., 2003b) o su estado copulatorio (Johnson, 2001).

Aunque faltan pruebas empíricas sólidas en favor de la ASH, la explicación del canibalismo sexual pre-copula como un síndrome de agresividad general de la hembra se apoya parcialmente en los indicios que sugieren una base genética de la

agresión (heredabilidad) (Riechert & Maynard-Smith, 1989; Riechert & Hedrick, 1993; Pruitt et al., 2008; Kralj-Fišer & Schneider, 2012), y en varios estudios que demuestran una correlación de la agresividad (voracidad de forrajeo) con el canibalismo sexual (Pruitt & Riechert, 2009a,b; Pruitt et al., 2008, 2011), así como una correlación entre la agresividad y otros rasgos conductuales (habilidad de caza, respuestas de escape a depredadores) que pueden definir la "personalidad" de las hembras (Riechert & Maynard Smith, 1989; Johnson & Sih, 2005, 2007; Pruitt et al., 2008; Kralj-Fišer & Schneider, 2012; Kralj-Fišer et al., 2012; Berning et al., 2012; Foellmer & Khadka, 2013).

V. EL CANIBALISMO SEXUAL PRE-CÓPULA EN EL ESTUDIO DE LA PERSONALIDAD ANIMAL

Desde un enfoque más amplio, los síndromes conductuales son análogos a **la personalidad animal o temperamento** (correlaciones conductuales consistentes entre contextos). La investigación emergente en este campo está desvelando que los síndromes conductuales son más frecuentes de lo que se creía, apareciendo entre los taxones inferiores de vertebrados y en invertebrados, en los que se presuponía limitado el repertorio conductual de sus individuos (Sih, 1993; Sih et al., 2003; Bell & Stamps, 2004; Bell, 2005; Quinn & Cresswell, 2005; Stapley & Keogh, 2005; Riechert & Hedrick, 1993; Kralj-Fišer & Schneider, 2012). En los últimos años esto ha despertado un gran interés debido a sus diversas implicaciones ecológicas y evolutivas (Sih et al., 2004a,b; Sih et al., 2012). Por ejemplo, a través de las correlaciones genéticas entre rasgos conductuales, los síndromes conductuales promueven respuestas selectivas correlacionadas sobre grupos de caracteres, entre los que se pueden encontrar rasgos que no son diana del proceso selectivo (Lande & Arnold, 1983), por lo que podrían limitar la evolución de determinados comportamientos. Esta aparente paradoja abre una ventana al estudio de los comportamientos aparentemente sub-óptimos que persisten en las poblaciones, tales como el canibalismo sexual pre-cópula, que parecen haber sido pasados por alto durante el estudio de los procesos evolutivos (ver Bell, 2007). Por último, cada vez son más numerosos los estudios en materias relacionadas con la ecología de la conducta y la biología evolutiva que han incorporado el concepto de síndromes conductuales para explicar importantes

cuestiones ecológicas, como la dinámica de poblaciones y las invasiones ecológicas (revisado en Sih et al., 2012), las interacciones parásito-depredador (revisado en Poulin et al., 2013), o la cognición animal (Sih & Del Giudice, 2012). Debido al compromiso extremo que supone el canibalismo sexual para las hembras (copular *vs* alimentarse de su consorte), estudiar este comportamiento puede revelar importantes patrones de cara a entender la evolución de la personalidad en animales invertebrados.

VI. LOS COSTES DEL CANIBALISMO SEXUAL PRE-CÓPULA EN LA HEMBRA. POLIANDRIA Y EL BENEFICIO DEL "REPARTO DE APUESTAS" (BET-HEDGING)

El canibalismo sexual pre-cópula, y particularmente el modelo no adaptativo, implica unos costes potencialmente altos sobre la eficacia biológica de las hembras, ya que éstas atacarían a machos indiscriminadamente, incluso si no se han apareado antes con ninguno o si hay limitación espermática que reduzca las posibilidades de fecundar sus huevos (Elgar, 1992; Arnqvist & Henriksson, 1997). Cuando una hembra dispone del esperma necesario para la fertilización, el pre-SC probablemente cause una menor variación de su eficacia biológica. La fecundación de los huevos es, por tanto, un punto de inflexión en el balance de costes y beneficios del pre-SC para la hembra, pero no garantiza la ausencia total de costes. Por ejemplo, en *L. hispanica*, aunque las hembras se hayan apareado, la fertilización de los huevos dentro del saco puede ser parcial, y el canibalismo indiscriminado impediría la transferencia del esperma necesario para fecundar los huevos que estén sin fecundar (Elgar, 1992). Algunos datos (Moya-Laraño, 1999) sugieren que podría haber un mecanismo de compensación de esta limitación espermática, por el cual la descendencia de las hembras que la padecen incrementaría su viabilidad alimentándose de los huevos no fecundados en el interior del saco.

En las especies caníbales sexuales, los beneficios directos del consumo del macho y los beneficios potenciales indirectos de la poliandria (las hembras se emparejan con varios machos) podrían interferir. Sin embargo, hasta la fecha el único estudio que ha intentado discernir entre ambos beneficios no encontró una relación significativa (Welke & Schneider, 2012). Se ha sugerido que uno de los

beneficios potenciales que podrían obtener las hembras poliándricas es la producción de descendientes con alta variabilidad de genotipos y fenotipos (Gillespie, 1974; Ridley, 1993; Yasui, 1998), lo cual podría favorecer el incremento de su viabilidad y supervivencia en ambientes heterogéneos (**Hipótesis del reparto de apuestas o "bet-hedging"**, en inglés) (Slatkin, 1974; Seger & Brockmann, 1987; Philippi & Seger, 1989; Watson, 1991, 1998; Fox & Rauter, 2003). Si hay un beneficio mediante bet-hedging, para una hembra que sea al mismo tiempo caníbal y poliándrica los machos serían recursos limitantes incluso si ya se han apareado, dado que perderían la posibilidad de incrementar la diversidad en su descendencia. El grado de poliandria es dependiente del acceso que tengan las hembras a los machos, y podría aumentar con la tasa de encuentros macho-hembra aunque, independientemente de la disponibilidad de machos, las preferencias de emparejamiento de las hembras podrían variar de acuerdo a determinadas circunstancias ambientales, demográficas o de sus historias de vida (Gowaty & Hubbell, 2005; Gowaty, 2013), e incluso algunas hembras podrían ser genéticamente más tendentes a la poliandria que otras (Eberhard, 1985; Ridley, 1988; Birkhead & Møller, 1998; Arnqvist & Nilsson, 2000; Gowaty, 2013). En definitiva, la disponibilidad de machos y el acceso que tengan a ellos, así como el tipo de emparejamiento de las hembras, pueden ser factores relevantes para determinar el coste del canibalismo sexual.

El éxito reproductor de una hembra virgen dependerá de sus oportunidades futuras de emparejamiento, que están relacionadas con la disponibilidad de machos en el ambiente. Una hembra virgen que canibaliza un macho en vez de copular con él asume un riesgo de limitación espermática, ya que podría no encontrar otro macho con el que emparejarse. Además, el canibalismo sexual puede provocar una disminución de la densidad de machos (Zimmerman & Spence, 1992; Moya-Laraño et al., 2003a) que favorezca la desviación de la proporción poblacional de sexos en favor de las hembras (Hurd et al., 1994) y disminuya las posibilidades de encontrar pareja y, por tanto, sería de esperar que la prevalencia del pre-SC no fuese muy alta (Newman & Elgar, 1991). Aunque se ha demostrado que los cambios de densidad y de proporción de sexos poblacional pueden variar de una especie a otra (Kasumovic et al., 2008), pocos estudios han examinado el papel de estos factores en las tasas de canibalismo sexual, y sólo algunos datos

sugieren que las hembras pueden ser más propensas al canibalismo cuando los machos son más abundantes (Newman & Elgar, 1991; Hebets, 2003; Johnson, 2005). En mántidos, se ha sugerido que podría haber un mecanismo genético que regulara la tendencia caníbal de las hembras en función de la disponibilidad de machos, que puede variar de forma estacional (Prokop & Vaclav, 2008), aunque no hay evidencia empírica de que esto ocurra (Prokop & Vaclav, 2005). En especies donde el canibalismo ocurre durante o tras la inseminación y existe una ventaja de paternidad por suicidio del macho, la abundancia de machos puede promover el canibalismo sexual, en parte por la fuerte competencia entre los machos y el bajo acceso a las hembras, ya que los machos se sacrificarán con mayor facilidad ante las hembras para obtener una ventaja de paternidad (Andrade, 2003; Andrade & Kasumovic, 2005; Fromhage et al., 2005; Snow & Andrade, 2005; ver también Vollrath & Parker, 1992). Sin embargo, estos ejemplos no sirven para ilustrar los efectos de la disponibilidad de pareja sobre las tasas de canibalismo sexual pre-cópula, y son necesarios experimentos que los documenten en la naturaleza y permitan discernir si las hembras son capaces de evaluar la abundancia de machos y de ajustarse a variaciones de la misma en el ambiente.

El rol de los machos

Para algunas hembras más agresivas, los machos podrían ser un recurso limitante como pareja incluso siendo abundantes, ya que en muchas especies caníbales sexuales los machos han desarrollado habilidades de escape y evitación de los ataques de las hembras que, de forma indirecta, podrían determinar sus preferencias hacia hembras menos peligrosas. Se han descrito numerosas estrategias que garantizan, en el peor de los casos, una reducción de los costes potenciales de cortejar a una hembra (revisado en Robinson, 1982), que incluyen desde la inmovilización de la hembra (Bruce & Carico, 1988) o el acercamiento a las hembras menos peligrosas (Elgar, 1992; Moya-Laraño et al., 2003a), cuando éstas están mudando (Foellmer & Fairbairn, 2003) o alimentándose de una presa recién capturada (Elgar & Fahey, 1996; Schneider & Elgar, 2001; Fromhage & Schneider, 2005), hasta cortejar a la hembra en momentos del día cuando el riesgo es menor (Moya-Laraño et al., 2004), o si han capturado antes una presa (Prenter et al., 1994a,b). Un estudio reciente llevado a cabo en el laboratorio mostró que los

machos pueden tener preferencias por las hembras que han atacado y consumido antes un macho, lo que podría tener un efecto significativo sobre las tasas globales de canibalismo sexual pre-cópula y sobre el éxito de emparejamiento de los dos sexos (Pruitt et al., 2014). Sin embargo, todavía no se ha investigado hasta qué punto estas estrategias de evitación del canibalismo pueden condicionar las tasas de canibalismo sexual en poblaciones naturales, aunque sería de esperar que el éxito o el fracaso de las respuestas de escape generaran variabilidad en la disponibilidad de machos y en la fecundidad y éxito reproductor de las hembras en función de sus niveles de agresividad.

Canibalismo sexual y poliandria. Un trade-off en el beneficio por "bet-hedging"

En relación a la hipótesis "bet-hedging" y los costes del pre-SC para las hembras ya emparejadas, puede haber un compromiso entre la poliandria y el canibalismo sexual si se cumple que: la poliandria aumenta la variabilidad de la descendencia, ésta mejora su viabilidad y por tanto la eficacia biológica de la hembra, y el canibalismo restringe los emparejamientos que maximizan el éxito reproductor de la hembra. Un ejemplo que ilustra bien este compromiso es el de *L. hispanica,* donde la variabilidad de tamaños de la descendencia puede ser el resultado de la dispersión en dos fases desde el ambiente materno, antes y después del invierno, lo que podría contribuir al incremento de su supervivencia durante la dispersión (Humphreys, 1983; Parellada, 1998; Moya-Laraño & Cabeza, 2003). Las madres proporcionan cuidado a las crías dentro del nido y las transportan sobre su abdomen hasta su dispersión, un período durante el cual su condición corporal aumenta. Sin embargo, las arañitas que se dispersan pronto no disponen de estas ventajas, que obtienen las crías que se dispersan tras el período de cuidados maternos. Los efectos de la poliandria sobre el tamaño de los descendientes en el nacimiento pueden ser determinantes para que haya crías de calidad variable, y podría ocurrir que las de mayor tamaño se dispersaran antes. La distribución de tamaños en dos fases podría aumentar la probabilidad de supervivencia de la progenie, ya que en promedio la proporción de supervivientes entre ambos picos de dispersión sería superior. Si las condiciones ambientales no son favorables y la tasa de mortalidad es alta durante uno de los picos de dispersión, al menos una proporción de las crías sobreviviría. La condición o masa corporal puede ser

importante para la supervivencia de las arañitas durante los períodos de mayor escasez de alimento (invierno), ya que en algunas arañas se ha visto que las crías en mejor condición tienen mayores probabilidades de sobrevivir y de madurar a adultos durante períodos de baja disponibilidad de presas (Schneider, 1995), alcanzando un mayor éxito reproductor (Schneider & Lubin, 1997). En algunas arañas, la poliandria no ejerce ninguna influencia sobre la fecundidad de la hembra ni sobre el tamaño y supervivencia de las arañitas (Welke & Schneider, 2012), aunque en otras estos beneficios pueden depender del sexo de las crías (Maklakov & Lubin, 2006), o incluso ser negativos sobre su tamaño, lo que influirá en su viabilidad durante la dispersión (Maklakov & Lubin, 2004).

Finalmente, habría que considerar los costes potenciales de la poliandria más allá del canibalismo para estimar si el beneficio mediante "bet-hedging" en la descendencia puede compensar dichos costes. Debido al conflicto sexual (Arnqvist & Rowe, 2005), los beneficios de la poliandria para el macho y la hembra pueden ser asimétricos. La frecuencia de cópulas de la hembra puede aumentar por encima del valor que maximiza su eficacia biológica, debido a que en los machos el óptimo ocurriría a una frecuencia superior por la competencia espermática y la paternidad compartida con otros machos (Birkhead et al., 1993; Birkhead & Møller, 1998; Simmons, 2001, 2005). Las consecuencias de la poliandria para las hembras pueden ser más favorables y contribuir significativamente a su éxito de fertilización (Simmons, 1988; Chapman et al., 1995; Newcomer et al., 1999; Arnqvist & Nilsson, 2000; McNamara et al., 2008; Gowaty et al., 2010), aunque también podrían influir negativamente sobre su eficacia biológica (Maklakov et al., 2005). Posiblemente, el balance de costes y beneficios de la poliandria dependa de la intensidad de la competencia espermática debida a los mecanismos de selección críptica de la hembra (Eberhard, 1996; revisado en Hasson & Stone, 2009). Asimismo, la presencia de machos puede ser perjudicial para la hembra si limita la disponibilidad de alimento, al acaparar una proporción de los recursos (presas), incrementar el riesgo de depredación de la hembra (Hurst et al., 1995; Arnqvist, 1997; Maklakov & Lubin, 2004) o, como en otros ejemplos de conflicto sexual, al disminuir el tiempo efectivo en que las hembras pueden dedicarse a conseguir alimento (Arnqvist & Rowe, 2005). Una hembra caníbal podría usar el pre-SC para

aliviar la limitación por el alimento e incrementar su descendencia, pero para poder hacerlo de forma segura (sin riesgo de limitación espermática), antes debería poder evaluar la disponibilidad de machos (sus oportunidades de emparejamiento futuras). Por ejemplo, en *L. hispanica*, debido a que el tiempo de cohabitación se correlaciona positivamente con el éxito reproductor de la hembra (Moya-Laraño et al., 2003a), las hembras que maduran más tarde y han cohabitado durante menos tiempo (Moya-Laraño et al., 2003a) pueden tener una capacidad limitada de acceso a los machos y evaluarán la disponibilidad como baja.

Cabe destacar asimismo que, aunque la discusión anterior se centra en el beneficio por "bet-hedging", los beneficios genéticos indirectos por elección de pareja (Zeh & Zeh, 1996, 1997, 2001; Tregenza & Wedell, 2000; Moya-Laraño & Fox, 2006) también pueden presentar un tipo de compromiso parecido con el canibalismo sexual. Si hay elección de pareja involucrada en las cópulas adicionales a la que asegura la fertilización de todos los huevos (e.g. Moya-Laraño & Fox, 2006), podría darse el caso de que esto se tradujese en una mejora en la eficacia biológica de la descendencia.

En resumen, en un ambiente donde los machos son un recurso limitante para las hembras, canibalizar en vez de emparejarse puede ser una práctica especialmente costosa; primero, por restringir la fecundación de los huevos y, segundo, por reducir las posibilidades de volver a aparearse y obtener una potencial ventaja a través de la poliandria. Si la evolución de la flexibilidad conductual no es muy costosa, parece razonable que las hembras fueran capaces de ajustar flexiblemente su tendencia caníbal en función de las características del ambiente, de la disponibilidad/limitación de alimento en el ambiente y de la disponibilidad de machos según sus preferencias y/o tipo de emparejamiento.

VII. LOS MODELOS BASADOS EN LOS INDIVIDUOS (IBMS)

La complejidad de las hipótesis involucradas en la evolución y mantenimiento del canibalismo sexual puede ser estudiada utilizando, además de mediante experimentación y método comparativo, simulación por computación. Los **modelos basados en individuos** (*Individual Based Models*, IBMs, en inglés) son simulaciones por ordenador mediante las cuales se pueden simular individuos

digitales con un genotipo y fenotipo determinados, hacerlos interaccionar entre ellos y estudiar el destino de determinados genes (y sus estrategias asociadas) a lo largo de las generaciones (DeAngelis & Mooij, 2005). Ello permite evaluar el valor adaptativo y el grado de estabilidad evolutiva de las diferentes estrategias, ya sean conductuales o vitales, de los individuos en diferentes escenarios ecológicos y a través de generaciones. Hasta la fecha, y a pesar de la potencia de dichos modelos, éstos no se han utilizado para investigar la evolución del canibalismo sexual.

Justificación y Objetivos

El canibalismo sexual puede ser un ejemplo de conflicto sexual extremo donde divergen los intereses reproductores de machos y hembras. Por un lado, el macho sirve a la hembra como fuente de esperma y alimento, y por otro, los machos que, en la mayoría de las especies animales buscan asegurar su paternidad apareándose con el mayor número de hembras posibles, deben desarrollar estrategias para evitar ser canibalizados durante sus encuentros sexuales con las hembras. Si el canibalismo sexual ocurre antes de la inseminación, las hembras se arriesgan a quedar sin emparejar. La anomalía de este conflicto extremo entre los intereses reproductores del macho y la hembra puede reflejar un proceso coevolutivo en marcha que aún no se ha resuelto completamente. A diferencia del canibalismo sexual post-cópula, el canibalismo sexual pre-cópula no puede ser considerado una estrategia reproductora del macho y hay que enfocarse en la búsqueda de los beneficios que obtienen las hembras y que expliquen por qué tienden a matar al macho en vez de aparearse con él. El canibalismo sexual puede tener un gran potencial como agente selectivo sobre diversos caracteres del macho y podría interferir en los procesos de selección sexual. Conocer, por tanto, los costes y beneficios del canibalismo sexual resulta de vital importancia para entender las causas del origen y mantenimiento de este comportamiento en la naturaleza.

A lo largo de esta tesis se exploran algunas premisas y predicciones de las principales hipótesis que se han propuesto para explicar el canibalismo sexual pre-cópula. El objetivo principal es determinar si el canibalismo sexual es un comportamiento frecuente en la naturaleza y si depende de condiciones ecológicas como la disponibilidad de machos y/o de alimento. También se pretende determinar si es o no un comportamiento adaptativo y si hay variabilidad entre las hembras en la tendencia al canibalismo. En base a los resultados obtenidos se discuten las posibles implicaciones ecológicas y evolutivas del canibalismo sexual, teniendo en cuenta los costes y beneficios de este comportamiento para las hembras y su potencial valor adaptativo.

Por otra parte, se investiga la relación entre la poliandria y la variabilidad fenotípica de la descendencia en una especie caníbal sexual, con el fin de esclarecer un posible compromiso entre la poliandria y el canibalismo sexual, dado que si la hembra obtiene potenciales beneficios de la poliandria a través de la producción de fenotipos diversos en ambientes heterogéneos, la limitación de machos debida al canibalismo sexual ejercerá también un coste al disminuir las posibilidades de poliandria. Por último, un modelo basado en los individuos (IBMs) de dos estrategias agresivas seguidas por las hembras permitirá conocer bajo qué condiciones ecológicas y de las historias de vida de éstas es más probable que evolucionen y se mantengan en poblaciones naturales diferentes estrategias de ataque a los machos. Las predicciones de dicho modelo serán contrastadas con los datos de la presente tesis.

Para responder a estas cuestiones se llevaron a cabo una serie de experimentos de campo y laboratorio en una población natural de la tarántula ibérica (*Lycosa hispanica*). Con los datos obtenidos se examinaron de forma directa dos de las hipótesis que se han propuesto para explicar el canibalismo sexual pre-cópula desde la perspectiva de la hembra. En primer lugar, la **hipótesis del forrajeo adaptativo** (Newman & Elgar, 1991), que predice que (1) la probabilidad de respuesta caníbal de una hembra será función del valor relativo del macho como presa o como pareja (y, por lo tanto, de la disponibilidad de machos y de la condición corporal y reproductora de las hembras), y (2) que la respuesta caníbal de una hembra tendrá efectos positivos sobre su eficacia biológica, incluso si la disponibilidad de alimento es alta. En segundo lugar, la hipótesis del **síndrome de agresión o personalidad por salpicadura agresiva** (aggressive spillover) (Arnqvist & Henriksson, 1997), que predice que habrá una correlación entre la agresividad de la hembra (voracidad hacia las presas) y su respuesta caníbal hacia un macho en el contexto de la cópula, y (2) que la "personalidad" agresiva implicará una limitación de la flexibilidad conductual en el contexto sexual.

Paralelamente, se contrasta la **hipótesis de elección de pareja** (Elgar & Nash, 1988), según la cual el canibalismo sexual es una forma de elección o rechazo de pareja que pueden usar las hembras para descartar a los peores machos para copular, y se cruza por primera vez dicha hipótesis con la hipótesis del síndrome

de agresión por salpicadura. Responder a esta cuestión nos permitirá conocer la importancia del fenotipo de los machos y de la "personalidad" de las hembras en la probabilidad de que un macho sea canibalizado o consiga aparearse, y por tanto en el impacto sobre el éxito reproductor tanto de machos como de hembras. Centrándonos en el sistema de apareamiento de las hembras (poliandria/monandria), se examinan los efectos de la poliandria de las hembras (emparejarse con varios machos) sobre la variación en el tamaño de las crías, y si es o no determinante en su éxito de supervivencia en un ambiente variable. Con ello se pretende contrastar la hipótesis del **reparto de apuestas** (bet-hedging) (Watson, 1991), según la cual la poliandria incrementaría la diversidad de genotipos y fenotipos de la descendencia y proporcionaría una ventaja de supervivencia y viabilidad en ambientes heterogéneos o impredecibles.

Por último, con datos procedentes de varios experimentos de campo (Moya-Laraño, 1999, 2002, 2003a,b), se parametrizan y corren simulaciones computacionales a partir del modelo Ungoliant (IBM). Este modelo permite contrastar la evolución de diferentes estrategias agresivas de las hembras bajo determinados escenarios ecológicos y proporciona información sobre la estabilidad y persistencia de cada una de ellas a través de generaciones sucesivas. Se contrastarán los escenarios de coexistencia o de invasibilidad de la estrategia del forrajeo adaptativo respecto a la estrategia de salpicadura agresiva (aggressive spillover) y se utilizarán los datos de esta tesis doctoral para corroborar algunas de las predicciones de las simulaciones.

En resumen, se pretenden acometer los siguientes objetivos:

1 – ESTUDIAR LA PREVALENCIA DE CANIBALISMO SEXUAL PRE-CÓPULA EN LA NATURALEZA

En el primer experimento de campo se realizaron manipulaciones experimentales de la densidad de machos y se estudiaron sus efectos sobre las tasas de canibalismo sexual y de cópulas de las hembras. Se predijo que las tasas de canibalismo sexual aumentarían con la disponibilidad de machos. También se predijo que la frecuencia de emparejamientos y cohabitaciones aumentaría con la densidad de machos.

2 – ESTUDIAR LOS BENEFICIOS NUTRICIONALES DEL CANIBALISMO SEXUAL PRE-CÓPULA SOBRE LAS HEMBRAS.

En un segundo experimento de campo llevado a cabo en la misma población se indujeron encuentros entre machos y hembras en cercados. Con el fin de contrastar la hipótesis de que el canibalismo sexual es beneficioso para las hembras, a la mitad de las hembras se les ofreció un macho para que se alimentaran de él. Por otra parte, a todas las hembras se les permitió copular con un macho, aunque sólo a la mitad se le ofreció hacerlo con más de uno (tratamiento de poliandria).

Se comparó el éxito reproductor de las hembras a las que se les había ofrecido un macho para que se alimentasen con el de las hembras que no habían recibido dicho macho. Puesto que todas las hembras disponían de abundantes presas naturales en los cercados, según las predicciones del **forrajeo adaptativo** las hembras que hubieran canibalizado un macho tendrían un mayor éxito de fecundidad que las hembras que no hubieran canibalizado ningún macho. Las estimas del éxito reproductor utilizadas fueron: peso de la puesta, número de crías, tamaño y condición corporal de las crías, éxito de la eclosión y proporción de huevos fecundados dentro de la puesta.

3 – ESTUDIAR EL CANIBALISMO SEXUAL COMO UN SÍNDROME DE AGRESIVIDAD DE LAS HEMBRAS Y SU EFECTO EN LA ELECCIÓN DE PAREJA

Para poner a prueba la **hipótesis del síndrome de personalidad por salpicadura agresiva (spillover)** se analizó la respuesta agresiva de las hembras adultas ante la presencia de machos, observando si atacaban al macho o copulaban con él. Asimismo, la tasa de engorde de las hembras subadultas ingiriendo presas naturales ofrecidas "ad libitum" permitiría desvelar si la agresividad de las hembras en el contexto de forrajeo (voracidad) predice su agresividad en el contexto sexual (canibalismo sexual), lo que evidenciaría que el canibalismo sexual es el producto de un síndrome de agresividad "spillover". Se investiga si esta correlación (síndrome agresivo) interfiere en la elección de pareja de la hembra, afectando a la selección de machos de diferente fenotipo.

4 – ESTUDIAR LOS EFECTOS DE LA POLIANDRIA EN LA VARIABILIDAD FENOTÍPICA DE LAS ARAÑITAS

En un experimento de laboratorio llevado a cabo con las crías de las madres procedentes del primer experimento de campo, se comparó el crecimiento y supervivencia de las crías de madres poliándricas (se aparearon en campo con varios machos) con el de las crías de madres monándricas (se aparean con un macho) a lo largo de varias fases de su desarrollo. Alterando el contenido de sus dietas se emuló el nivel de variabilidad ambiental (imitando años buenos y años malos) al que las crías probablemente deban hacer frente durante su dispersión. Se predijo que la progenie de las hembras poliándricas sería más variable en tamaño y crecimiento que la de las hembras monándricas, y que en promedio el éxito de supervivencia de las crías sería mayor en las primeras. La apuesta de las madres poliándricas por la diversidad de tamaños de sus crías propiciaría una ventaja de supervivencia ante la heterogeneidad ambiental impredecible (**hipótesis del reparto de apuestas o "bet-hedging"**).

5 – CONSTRUIR Y EJECUTAR UN MODELO DE EVOLUCIÓN DE LAS ESTRATEGIAS DE CANIBALISMO SEXUAL EN LAS HEMBRAS Y CORROBORAR ALGUNAS PREDICCIONES CON LOS DATOS DISPONIBLES

Ungoliant es un modelo basado en los individuos desarrollado para investigar el canibalismo sexual. La combinación de simulaciones computacionales con datos de campo y laboratorio puede aportar información relevante sobre el canibalismo sexual, al predecir las estrategias que tienen mayor probabilidad de persistir evolutivamente a lo largo de generaciones (Estrategias Evolutivamente Estables – Maynard-Smith 1982). Este modelo fue utilizado para investigar qué parámetros ecológicos (tasa de encuentros macho-hembra, disponibilidad de alimento, etc.) y de las historias de vida de las hembras (tiempo de maduración) favorecerían la prevalencia y estabilidad del canibalismo sexual indiscriminado (antes de que la hembra copule por primera vez) (Arnqvist & Henriksson, 1997) respecto al canibalismo que podríamos llamar más cauteloso (copular primero y canibalizar después a los siguientes machos que se presenten), y si ambas estrategias podrían coexistir en una población. El grado de estabilidad del

canibalismo sexual como un síndrome de agresividad de las hembras puede depender de la proporción de hembras que siguen una u otra estrategia. Con los nuevos datos aportados por los experimentos de campo de esta tesis se pretende contrastar si las predicciones del modelo se cumplen.

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MANUSCRITOS

MANUSCRITO I

Sexual Cannibalism: High Incidence in a Natural Population with Benefits to Females

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Publicado en:

PLoS ONE (2008) 3(10)

Resumen

Antecedentes. El canibalismo sexual puede ser una forma de conflicto sexual extremo en el que el beneficio para las hembras de comerse al macho puede ser mayor que el de aparearse con él, mientras que los machos tienden a evitar a estas hembras caníbales para incrementar su eficacia biológica. Entender con profundidad el significado adaptativo del canibalismo sexual se complica debido al desconocimiento actual de su prevalencia en la naturaleza. Además, hay serias dudas sobre el valor alimenticio de los machos, probablemente porque la mayoría de los estudios que han intentado documentar los beneficios del canibalismo sexual para la hembra se han llevado a cabo en el laboratorio con presas alternativas no naturales. En definitiva, para entender mejor la ecología y la evolución del canibalismo sexual se requieren experimentos de campo que documenten su prevalencia y los beneficios que obtienen las hembras.

Metodología/Principales resultados. Se llevaron a cabo varios experimentos de campo con la tarántula mediterránea (*Lycosa tarantula*), una araña lobo constructora de madrigueras, con el fin de abordar las cuestiones mencionadas. A una tasa natural de encuentros entre machos y hembras, aproximadamente un tercio de las hembras de *L. tarantula* canibalizaron un macho. La tasa de canibalismo sexual aumentó con la disponibilidad de machos, y las hembras fueron más propensas a matar y consumir un macho que se acercaba a su nido si se habían apareado antes con otro macho. Encontramos que las hembras que se alimentaban de un macho obtenían ventajas de fecundidad, ya que hacían antes la puesta, producían un 30% más de descendientes por cada saco de huevos y éstos tenían una mejor condición corporal. La progenie de las hembras caníbales se dispersó antes desde el nido materno y su tamaño fue mayor al final de la estación reproductora, comparado con las crías de las hembras no caníbales.

Conclusiones. En la naturaleza, una proporción significativa de hembras de *L. tarantula* mata y consume a los machos que se aproximan al nido con la intención de copular. La probabilidad de que esto ocurra es mayor si la hembra se ha apareado previamente. Las hembras caníbales tienen mayores tasas reproductoras y producen descendencia de mayor calidad que las hembras no caníbales. Nuestros hallazgos sugieren que las hembras de *L. tarantula* están limitadas nutricionalmente en la naturaleza y que los machos son una presa de gran calidad en sus dietas. Los resultados de estos experimentos de campo apoyan la hipótesis de que el canibalismo sexual es adaptativo para las hembras.

***Palabras clave**: Lycosa tarantula, canibalismo sexual, desequilibrio nutricional, forrajeo adaptativo, sex ratio, eficacia biológica*

Abstract

Background. Sexual cannibalism may be a form of extreme sexual conflict in which females benefit more from feeding on males than mating with them, and males avoid aggressive, cannibalistic females in order to increase net fitness. A thorough understanding of the adaptive significance of sexual cannibalism is hindered by our ignorance of its prevalence in nature. Furthermore, there are serious doubts about the food value of males, probably because most studies that attempt to document benefits of sexual cannibalism to the female have been conducted in the laboratory with non-natural alternative prey. Thus, to understand more fully the ecology and evolution of sexual cannibalism, field experiments are needed to document the prevalence of sexual cannibalism and its benefits to females.

Methodology/Principal Findings. We conducted field experiments with the Mediterranean tarantula (*Lycosa tarantula*), a burrowing wolf spider, to address these issues. At natural rates of encounter with males, approximately a third of *L.tarantula* females cannibalized the male. The rate of sexual cannibalism increased with male availability, and females were more likely to kill and consume an approaching male if they had previously mated with another male. We show that females benefit from feeding on a male by breeding earlier, producing 30% more offspring per egg sac, and producing progeny of higher body condition. Offspring of sexually cannibalistic females dispersed earlier and were larger later in the season than spiderlings of non-cannibalistic females.

Conclusions/Significance. In nature a substantial fraction of female *L.tarantula* kill and consume approaching males instead of mating with them. This behaviour is more likely to occur if the female has mated previously. Cannibalistic females have higher rates of reproduction, and produce higher-quality offspring, than non-cannibalistic females. Our findings further suggest that female *L.tarantula* are nutrient-limited in nature and that males are high-quality prey. The results of these field experiments support the hypothesis that sexual cannibalism is adaptive to females.

Keywords: *Lycosa tarantula, sexual cannibalism, nutritional unbalance, adaptive foraging, sex ratio, fecundity fitness*

Introduction

Sexual cannibalism, a behaviour in which one member of a courting or copulating male-female pair consumes the other, may be widespread among some arthropods (Elgar 1992). A female can kill a male either before, during, or after mating (Elgar 1992; Elgar & Schneider 2004). Pre-mating sexual cannibalism entails extreme sexual conflict: females may accrue nutritional benefits by killing and consuming approaching males instead of mating with them (Newman & Elgar 1991), whereas males, who must approach females in order to copulate, risk being killed by the females they approach (Schneider & Lubin 1998). Pre-mating sexual cannibalism may also be a form of mate choice, in which females kill and consume males that they estimate to be of low quality as sires (Elgar 1992; Prenter et al. 2006). This paper deals with the foraging benefits of pre-mating sexual cannibalism (Newman & Elgar 1991).

The adaptive value of pre-mating sexual cannibalism is controversial largely because there is little supporting evidence that killing and eating a potential mate benefits females at all (Newman & Elgar 1991; Arnqvist & Henriksson 1997; Johns & Maxwell 1997; Maxwell 2000; Johnson 2001; Schneider & Elgar 2002; Fromhage & Schneider 2003). Fuelling the controversy is the fact that most studies seeking to determine the adaptive value of sexual cannibalism to females are not conducted under natural conditions (Elgar & Nash 1988; Arnqvist & Henriksson 1997; Maxwell 2000; Johnson 2001; Schneider & Elgar 2002; Fromhage & Schneider 2003) and there are only few correlational studies in the field (Moya-Laraño et al. 2003a,b). Knowing the rate at which sexual cannibalism occurs in nature is crucial to understanding its ecological and evolutionary significance; however, the rate of sexual cannibalism in nature is largely unknown (Elgar 1992; Wise 2006). High rates of sexual cannibalism in staged encounters in the laboratory may be a laboratory artefact. Jackson (1980) proposed that the actual rate of sexual cannibalism among spiders in nature may not be as high as previously thought (Jackson 1980). For instance, if females in the laboratory lack some essential nutrients, or if males in a cage cannot escape the female's attack, observed rates of cannibalism may be artificially high. When sexual cannibalism is

pre-copulatory, natural selection should favour males that avoid cannibalistic females, leading to adaptive male behaviors such as approaching females at times of the day or season when they are less aggressive (Moya-Laraño et al. 2004; Fromhage & Schneider 2005), or being able to recognize, and preferentially approach, the less aggressive females in the population (Moya-Laraño et al. 2003a). The circumstances of staged encounters in the laboratory often do not permit the expression of such adaptive male behaviours.

Laboratory experiments on sexual cannibalism have never been conducted with a spectrum of natural prey as alternative food sources. The quality and amount of prey in a laboratory experiment may be very different from that in the wild. This is not a trivial issue, because increasing numbers of studies reveal that differences in prey quality may affect the survival, growth and fecundity of predatory arthropods (Uetz 1992; Toft & Wise 1999; Mayntz & Toft 2001; Wilder & Rypstra 2008), and that predatory arthropods may feed differentially according to nutrient needs (Greenstone 1979; Mayntz et al. 2005). Thus, the quality of alternative prey in a female's environment may influence her proclivity towards sexual cannibalism.

Therefore, in order to understand more thoroughly both the ecological implications of sexual cannibalism and its evolutionary origins and evolutionary maintenance, i.e. whether or not it is likely to be an evolved, adaptive behaviour, field experiments are needed to document that 1) pre-mating sexual cannibalism occurs at substantial rates in nature, and 2) females that are exposed to the spectrum of alternative prey present in their natural environment benefit from sexual cannibalism.

The Mediterranean tarantula (*Lycosa tarantula*) is a territorial and cannibalistic burrowing wolf spider (Moya-Laraño et al. 2002a) that is well suited for experiments on pre-mating sexual cannibalism. First, field experiments have established that female *L.tarantula* are food-limited in nature (Moya-Laraño 2002; Moya-Laraño et al. 2003b). Second, observations in nature and field experiments reveal that female *L.tarantula* can be sexual cannibals (Moya-Laraño et al. 2002a; Moya-Laraño et al. 2003a). Third, indirect evidence from a field experiment (Moya-Laraño et al. 2003b) suggests that females appear to compensate for the effects of

food limitation experienced as juveniles by cannibalizing males, although it remains to be established conclusively that the apparent compensation for food limitation is actually due to sexual cannibalism. Fourth, sexual size dimorphism in *L.tarantula* is relatively small (Fernández-Montraveta & Moya-Laraño 2007; Foellmer & Moya-Laraño 2007), which makes males a potentially good meal for females (Moya-Laraño et al. 2003b), especially in comparison with natural prey, which are on average several times smaller (Moya-Laraño et al. 2002a). And lastly, females can easily be induced to take up residence in standardized burrows constructed at pre-determined locations in the field, which greatly facilitates density manipulations and behavioural observations (Moya-Laraño et al. 2002a).

Here we present the results of three field experiments and a supporting laboratory experiment with *L.tarantula* designed to reveal whether or not pre-mating sexual cannibalism (1) occurs in nature at natural rates of encounter between males and females; (2) is relatively frequent, or instead, is a rare occurrence; (3) is more frequent when males are more abundant; and (4) increases female fitness by enhancing fecundity and/or offspring quality. In the first field experiment we manipulated male availability by establishing three different densities of males in large plots in which females at natural density were exposed to natural densities of alternative (i.e. non-*L.tarantula*) prey. In this experiment we measured both the rate of sexual cannibalism and the frequency of mating. In a second field experiment, individual females in enclosures approximating female territory size (Moya-Laraño et al. 1998; Moya-Laraño 1999) were provided with natural prey at rates mimicking rates of supply in nature, with half of these females also being permitted to feed on a cannibalized male. A third field experiment, and a laboratory experiment, compared the performance of the progeny of females that had fed on a male in addition to natural prey, to that of the offspring of females that had consumed natural prey but no male *L.tarantula*. These experiments revealed that sexual cannibalism by female *L.tarantula* occurs frequently in nature, and that females that have fed on natural heterospecific prey still obtain clear fitness benefits from also including a single male *L.tarantula* in their diet.

Materials and Methods

1. Species and study site

The Mediterranean tarantula (*Lycosa tarantula*) is a burrowing wolf spider with a 2-year life cycle (Orta et al. 1993; Moya-Laraño 1999). Juvenile spiders wander until they are one-year old, at which time they settle in burrows (Moya-Laraño et al. 1996). Maturation occurs at 21–22 months of age and the mating season takes place between June and August. All field experiments were conducted outside the border of the Cabo de Gata-Níjar Natural Park, Almería, in southeastern Spain, on the same study site in which some of the previous studies with this species were performed (Moya-Laraño et al. 2002a; Moya-Laraño et al. 2003a; Moya-Laraño et al. 2004).

2. Field Experiment 1: Natural rates of pre-copulatory sexual cannibalism and the influence of male availability on cannibalism rate

2.1. *Experimental design.*

Sub-adult spiders of both sexes were collected from nearby areas from 10 to 25 May 2005. Virgin females (n = 72) were added to nine 12×12-m plots that were set in a 3×3 array of 50×50 m and from which all *L.tarantula* had been removed. Eight females were added to each plot by introducing them into artificial burrows (Moya-Laraño et al. 2002a) equidistantly spaced within the plot. With this procedure we assured that all plots had identical female densities with the same spatial dispersion pattern. Around the entrance of natural burrows the spider constructs a turret, which has been shown to improve spider survival (Williams et al. 2006). The turret was removed from the original burrow from which the captured spider had been removed, and was placed around the mouth of the artificial burrow. These burrows, which were constructed entirely of materials that spiders use to make natural burrows, have been found to promote natural burrowing behaviors, as all introduced spiders remain in them, commence excavating them further to meet their own requirements, and immediately fix the turret with silk after being introduced into the burrow by us. A previous experiment (Moya-Laraño et al. 2002a) with these burrows that included a control

treatment for the effect of the burrow itself showed that the artificial burrow had no effect on spider mortality. The burrow density utilized in this experiment was similar to previous estimates of female density in this population (Moya-Laraño 1999). Each plot was randomly assigned to one of three male-availability treatments: Low (8 males), Medium (16 males) and High (32 males). The original goal was to establish a 1:1 sex ratio for the Medium treatment, with 4 and 16 males in the Low and High treatments, respectively. However, unexpected high mortality of males soon after the additions, probably from bird predation, forced us to add additional males to all treatments in order to achieve natural rates of encounter between males and females. With this modification we established rates of encounter between males and females in the Medium treatment that were very close to those observed in nature (see Discussion). From 25 May to 17 July we added 65 males of known virginity (collected as subadults from the surrounding area, placed in artificial burrows outside the study plots, and daily checked for maturation) and 70 males of unknown mating history collected as adults from the surrounding area (18–19 males per week for 7 weeks). Males from both groups were randomly assigned to experimental treatments with the restriction that the ratio of virgin males to males of unknown mating history was the same for each plot. Males were released in the plots at night in order to prevent excessive exposure to heat. We placed 5 bricks in each plot (one in the centre and one in each corner) as shelter from excessive heat for recently introduced males.

A 30-cm wide continuous trench (15 cm in depth) along the perimeter of each plot housed two contiguous pitfall traps made of sheet metal, which made it difficult for trapped arthropods to escape. The trench traps were emptied at dawn and dusk, and also during the day when conditions made it likely that captured animals would become overheated if left in the traps all day. The continuous monitoring of two pitfall traps allowed us to document and control the natural flow of walking migrating prey in and out of the plots. All arthropods >0.5 mm (and thus potential prey of *L.tarantula*) that were captured in the outer pitfall trap were introduced into the plots, and prey found in the inner trap were released outside the plot. Since scorpions are known to be important predators of female *L.tarantula* (Moya-Laraño et al. 2003a; Williams et al. 2006), we did not introduce into the plots scorpions that were trapped in the outer trench traps. At

the beginning of the experiment a single scorpion killed and consumed two females, which convinced us that it would be too risky for the experiment to allow scorpions to immigrate into the plots. All *L.tarantula* males found in the inner trap were returned to the centre of the plot. Predation by foxes (*Vulpes vulpes*), a major source of mortality for *L.tarantula* (Moya-Laraño 2002; Moya-Laraño et al. 2002a), was prevented by installing a 50-cm electric fence around the 0.25 ha area containing the nine plots. However, bird predation, which was presumably very high on males as judged by the relatively low survival times (mode = 5 days), was not prevented by this design.

2.2. *Marking and monitoring.*

Before being placed in the plot, each spider was weighed (nearest 0.01 g) and its carapace (CW) and abdomen (AW) widths were measured (nearest 0.01 mm). Each spider was uniquely marked–females with markings on the legs (Moya-Laraño, 1999; Moya-Laraño et al. 2003b), males with either leg markings and bee tags (of which we used two colors, orange and green), or only with leg markings. An evaluation of male survival (defined as days remaining in the plots) using survival regression analysis (Moya-Laraño & Wise 2000) revealed that the three different markings (orange or green bee tags or marking on the legs only) did not differentially affect male mortality (Accelerated Failure Time Survival Model with Weibull distribution, $\chi^2_2 = 2.8$; $P = 0.246$). Since release time had a significant effect on mortality, with males that were released later in the season surviving for a shorter time, we included release time as a covariate in the model ($\chi^2_1 = 3.9$; $P = 0.049$).

2.3. Behavioural data.

Throughout the season each female burrow was closely monitored for cannibalistic and mating behaviours. A male remains near the entrance of a female's burrow up to several days (“cohabitation”), moving slightly farther from the entrance at night, when the female comes out to hunt prey (Moya-Laraño et al. 2004). Mating occurs inside the burrow, but only during daylight hours (Moya-Laraño et al. 2003a,b; Moya-Laraño et al. 2004; Fernández-Montraveta &

Cuadrado, 2003). Because of this known activity pattern, we expected to detect pre-copula cannibalisms mainly at night. Preliminary observations suggested that the handling time of cannibalized males is several hours. Thus, in order to maximize the chances of observing cannibalism (Moya-Laraño et al. 2003a), every female was visited once each night and again early in the morning (see below). Mating and cohabitation were monitored during the day by visiting females at 1-h intervals from 8 am to 3 pm, the time window when most copulations occur in nature (Moya-Laraño et al. 2003a). This observation schedule provided a nearly complete picture of the sexual and cannibalistic activities of the spiders in the plots.

2.4. Statistical analyses

Most tests were performed using the General Linear Model (GLM) applied to plot means. Since we predicted that mating and cannibalism rates ("rate" defined as the mean number of occurrences per plot or per treatment) would increase linearly with male availability, we used orthogonal linear contrasts for testing planned comparisons. We first ran all analyses including the spatial coordinates of the plots (X,Y) in order to determine if a spatial autocorrelation might contribute to patterns that were otherwise being ascribed solely to treatment effects. Because none of the coordinates was significant in any of the tests (all $P>0.3$), and the results remained qualitatively the same when they were removed, we removed the spatial coordinates from the statistical models presented here. For hypotheses in which female covariates needed to be included in the model, we nested plot within treatment in order to control for plot effects. We included plot as a fixed factor because it has been shown that when the number of treatment levels is below 10 and the potentially random effect does not absorb the fixed effect, the inclusion of random factors results in highly unreliable estimates (Collett 2003; Piepho et al. 2003). Since the dependent variable in the model was discrete (e.g. number of cannibalistic events, number of matings), we used Generalized Linear Models with Poisson distributions controlled for overdispersion (Moya-Laraño & Wise 2007). We used STATISTICA 8.0 except for orthogonal contrasts in Poisson GLM, for which we used SAS 9.0.

3. Field Experiment 2: Contribution of sexual cannibalism to female reproductive success

3.1. Experimental design.

This experiment was conducted in the following year (May–November 2006). To ensure the virginity of mature females that were used in the experiment, sub-adult females (n = 80) were placed in artificial burrows (see above) and isolated in field enclosures 1 m×1 m×30-cm high, an area that approximates the smallest territory size of a female in this population (Moya-Laraño et al. 1998; Moya-Laraño et al. 2002a). The enclosures were then covered with 0.5-cm mesh screening to prevent bird predation. This design allowed us to control the availability of natural prey species, and to manipulate the nutritional benefits of cannibalism by removing a recently killed male from the jaws of half of all females that had killed a male.

3.2. Induced mating.

An adult male collected from the field (i.e., of unknown mating history) was introduced to the enclosure of every female one week after she had moulted to maturity. We removed the male and introduced a new male daily until the first complete mating occurred. The aim was to ensure that all females mated, so that it would be possible to test if the cannibalism treatment (described below) altered female reproductive success. Males, which had been randomly assigned to each of the 80 enclosures containing the female burrows, were released daily into a 20×20×10-cm metal cage placed on top of the burrow entrance; 8 female mating trials were run per day. This male enclosure ensured normal male courtship, as normal cohabitation distances during the night, the time prior to mating, are 15–20 cm (Moya-Laraño et al. 2004). On the first introduction of a male, some females cannibalized their potential partner instead of copulating with him. All males found dead in the female's jaws were removed and weighed. Statistical models were run including this extra-male intake as a covariate, but because this variable was never significant (P's>0.2), we excluded it from the final analyses. The average mass extracted by females in these "secondary" cannibalistic attacks was 0.12±0.03 g, which is ca. one-third the mass of a single natural prey item (see

below). Females that killed the male were offered a different male the next day and so on until a complete mating was achieved. Males were never used more than once.

This experiment was part of a larger "polyandry" experiment in which half of the females were offered 4 additional males as potential mates, but were not allowed to cannibalize them. The effect of this additional treatment and its interaction with the cannibalism treatment were not significant for any of the variables measured here (*P*'s>0.16). These results will be published separately as part of another study on sexual conflict.

3.3. Cannibalism treatment

One week after each female had first mated she was presented with a male that had been kept in a freezer for 10 minutes to make him lethargic and susceptible to female attack. Females were then randomly assigned to one of two cannibalism treatments: Cannibalistic or non-cannibalistic. In the non-cannibalistic treatment, the male was removed from the female's jaws 10 minutes after being killed, thus preventing the female from cannibalizing him. Females in the non-cannibalistic treatment extracted on average 7.2±0.4% of the male mass during this 10-minute period. In contrast, in the cannibalistic treatment females were allowed to completely consume the males they had killed and presumably consumed most of the male. Assessing how much remained after allowing the experimentally cannibalistic females to consume the male was not feasible because only a portion of the remains is left outside the burrow; the rest is deposited inside the burrow, making full recovery unlikely. Once a week females in both treatments were given 10 of the most frequently consumed natural prey items: darkling beetles (Tenebrionidae) and woodlice (Isopoda) (Moya-Laraño et al. 2002a) in a proportion that depended on natural availability and which changed from week to week. Since the natural rate of feeding is lower than one prey item per night (Moya-Laraño 1999), this rate of prey supplementation should have mimicked an unlimited food supply. Female feeding behaviour corroborates the prediction that this rate of prey supply provided an excess of prey. We counted and weighed the prey that remained alive in the enclosures of 7 experimentally non-

cannibalistic females that had laid an egg sac. The average number of live prey in each enclosure was 35±2.8 (SE). The average weight was 0.31±0.03 g, which translates into an average total biomass per enclosure of 10.6±0.9 g, which is about 7 times the mass of a single adult male *L.tarantula* (1.47±0.02 g; N = 139).

3.4. Fecundity estimates.

After mated females have acquired enough food resources for egg development, they seal the mouth of their burrow with silk, probably as a defence against predators (Moya-Laraño 1999). Females at this stage were removed from their burrows and isolated in extractable PVC burrows (20 cm×2.5-cm diameter) until their spiderlings had emerged from the egg sac. The mouth of these burrows, which were located outside the experimental plots, was covered with 0.5 mm-mesh netting that allowed us to monitor egg laying and spiderling hatching without disturbing the female. Hatchlings were counted and a randomly selected sub-sample (n = 10 per female) was weighed and their carapace widths (CW) measured (Moya-Laraño 2002). The remaining offspring were either released back into the field or used in another experiment testing for offspring performance (see below). Females inside burrows suffered high mortality between the stages of egg-sac development and egg hatching, probably from high amounts of rainfall. Thus we were able to assess estimates of reproductive fitness for only 56% of the females (n = 45). The fitness estimates were egg sac mass, number of spiderlings, spiderling size (CW), spiderling body condition (the residuals from the linear regression of the cubic root of mass on carapace width), hatching success (whether or not the spiderlings were able to break out of the egg sac), and hatching rate (the ratio of the number of spiderlings hatched to the total number of eggs laid).

3.5. Statistical analyses.

We used GLM to test for differences between treatment groups. For binary response variables we used GLM with a binomial error distribution, and for discrete response variables (counts) we used GLM with a Poisson distribution controlled for overdispersion (Moya-Laraño & Wise 2007). Since body size did not affect either the mass of the egg sac nor the number of offspring, we did not

include it as a covariate for our final analyses. STATISTICA 8.0 was used for all analyses.

4. Field Experiment 3: Survival and growth of dispersing offspring of cannibalistic and non-cannibalistic females

As a means to evaluate effects of the cannibalism treatment on offspring performance, we used hatched spiderlings from the above experiment. A sub-sample of full-sib spiderlings from 31 females in the cannibalistic and non-cannibalistic treatments (16 and 15 females, respectively) was returned to the 1×1-m field enclosures used to house the females before they laid an egg sac. Low fecundity in some females and the need to allocate 10 spiderlings for body measurements (see above) prevented us from utilizing offspring from all the females that survived and laid egg sacs. In order to prevent spiderlings from aggregating in the old female burrow, we filled it with stones and dirt. We introduced spiderlings at two densities (high, 42/m^2; and low, 21/m^2). This range in density of dispersing offspring was based upon previously collected data on the density and fecundity of females in this population of *L.tarantula* (Moya-Laraño 1999), and also data from the current study. The spiderling-density treatment was crossed with the cannibalism treatment that their mothers experienced (cannibalistic-high, n = 9; cannibalistic-low, n = 7; non-cannibalistic-high, n = 9; non-cannibalistic-low, n = 6). Due to variation in the timing of spiderling dispersal from the mother, the 1 m×1 m-plots with dispersed spiderlings were set up from 19 August through 10 November 2006; the experiment ended 6 December 2006. At the end of the experiment, all surviving spiderlings were removed, weighed and measured (CW and AW). In order to uncover family differences in growth rates (either from maternal effects distinct from having fed experimentally on a male, or from genetic differences), we nested dam (mother) as random factor within the cannibalistic treatment in a GLM. STATISTICA 8.0 was used for all analyses.

5. Laboratory Experiment 1: Rates of cannibalism among offspring of cannibalistic and non-cannibalistic females

Field and laboratory microcosm experiments have demonstrated that spiderling-spiderling cannibalism can be a significant factor regulating densities of wolf spiders (Wagner & Wise 1996, 1997). In the laboratory we tested whether or not the larger size attained by the offspring of cannibalistic females, due to their earlier hatching and dispersal, gave them an advantage over the offspring of non-cannibalistic females in spiderling-spiderling encounters. We used spiders that had survived to the end of Field Experiment 3. One offspring of a cannibalistic female was paired with an offspring of a non-cannibalistic female in 9-cm Ø Petri dishes (n = 31) that contained a 2-mm deep substrate of fine soil from the study site. We started the experiment in the afternoon and checked for cannibalism every hour for 12 hours. The data analysis was complicated by the need to include more than one offspring from the same mother. We first present the results of a G-test done on the data ignoring genetic relatedness. Then, in order to remove possible problems of interpretation due to pseudoreplication, we employed a randomization procedure that consisted of selecting at random one individual from each Petri dish and averaging the response (cannibalistic "1" or non-cannibalistic "0") across mothers, using each mother as a replicate, for analysis with the Mann-Whitney U-test. This non-parametric test was used because averages constructed from 1's and 0's are highly skewed. STATISTICA 8.0 was used for all analyses.

Results

Field Experiment 1: Natural rates of pre-copulatory sexual cannibalism and the influence of male availability on cannibalism rate

In large field plots that enclosed female *L.tarantula* in burrows at natural densities and that spanned three different male-density treatments, a third of the females (24/72) cannibalized at least one male; five females cannibalized two

males. Cannibalism was almost entirely pre-copulatory (28/29 cannibalistic events).

Females did not tend to attack males indiscriminately–mated females were more likely than virgin females to kill a potential mate. Among those females who killed a potential mate before mating and who also mated at least once during the experiment (20 out of 24 cannibalistic females), mated females showed a 3.4× higher rate of pre-mating sexual cannibalism than virgins (Wilcoxon matched-pairs test, Z = 3.2, P = 0.0015). Only 15% (3/20) of this group of cannibalistic females killed a male before their first mating (Fig. 1). This result is not likely due to a difference in how many males were available for virgin and mated females, as the numbers of males that were released in the plots before (10.9±1.6) and after (14.4±1.6) each female mated for the first time were only 1.4× higher after mating and not significantly different (Wilcoxon matched-pairs test, Z = 1.1, P = 0.29). In addition, the number of males released before or after mating was not significantly associated with the number of cannibalistic events before or after mating (both Spearman correlations r_S<0.25; P>0.27). We also tested whether there were significant effects of plot or the male-availability treatment on whether or not mating status affected the probability that a female was cannibalistic, and found no significant effects (both P's in the model>0.45). In the above analyses, 3 cannibalistic females could not be included because they killed the male while they were virgin and subsequently never mated. Thus, the number of virgin females that killed a male is 8% of all virgins (6 out of 72, the total number of virgin females introduced into the plots), and the number of females who first killed a male when they were virgins is 25% of all cannibalistic females (6/24).

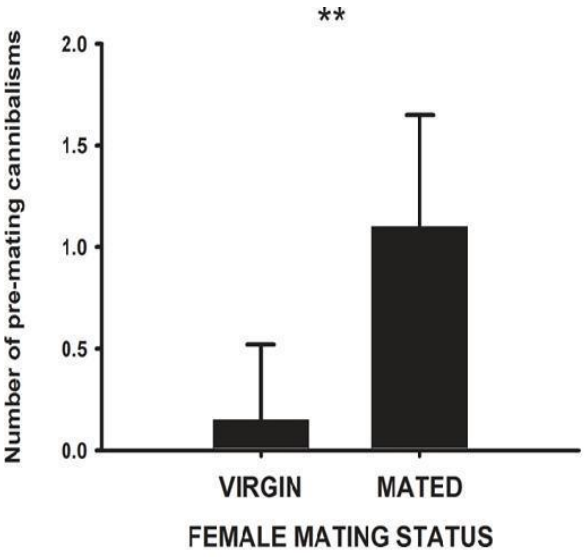

Figure 1. Female mating status affects the rate of pre-copulatory sexual cannibalism in *L.tarantula*. Rates of pre-mating sexual cannibalism (number of cannibalistic events per female) for 20 females that cannibalized at least one male. We compare the mean number of cannibalistic events for the same females as virgins and after they had mated once. Bars and error bars represent mean and standard errors, respectively. **, P<0.01. Refer to the text for more details of the statistical analysis.

Our manipulation of male densities revealed that as the number of males per female in the population increased, the rate of sexual cannibalism and the number of matings per female also increased (Fig. 2A, C). Differences among treatment groups are significant for all response variables (*P*'s<0.05, GLM). For simplicity, however, we present results only for the linear trends, i.e. the expected increase in a response variable with increasing male availability. The rate of cannibalism (mean number of cannibalistic events per plot) increased linearly from the low to high male-density treatments (orthogonal linear contrast, $F_{1, 6}$ = 17.4, P = 0.006, Fig. 2A), as did the number of cannibalistic females per plot (orthogonal linear contrast, $F_{1, 6}$ = 30.0, P = 0.002, Fig. 2B). The mean number of copulations per plot also displayed a linear trend (orthogonal linear contrast, $F_{1, 6}$ = 13.5, P = 0.01; Fig. 2C). The rate of cohabitation (the number of males observed within 20 cm of the female burrow) is a good estimate of the number of male-female interactions (Moya-Laraño et al. 2003a; Moya-Laraño et al. 2004) . This parameter also increased linearly with male density (orthogonal linear contrast, $F_{1, 6}$ = 42.9, P = 0. 001; Fig. 2D).

The rate of cannibalism increased linearly with male availability in excess of the higher encounter rates of males with females at higher male densities. A Poisson GLM with plot nested within treatment and controlling for the estimated per capita rate of female-male interactions (i.e. including the cohabitation rate as a covariate), showed that the interaction rate*per se* did not significantly affect the

rate of sexual cannibalism ($F_{1,52}$ = 0.3, P = 0. 615). Furthermore, there was still a significant treatment effect after the effect of cohabitation rates had been removed (orthogonal linear contrast, $F_{1,52}$ = 6.5, P = 0.01), indicating that the higher rate of cannibalism in plots with more males did not occur solely because the encounter rate between predators (females) and prey (males) was higher.

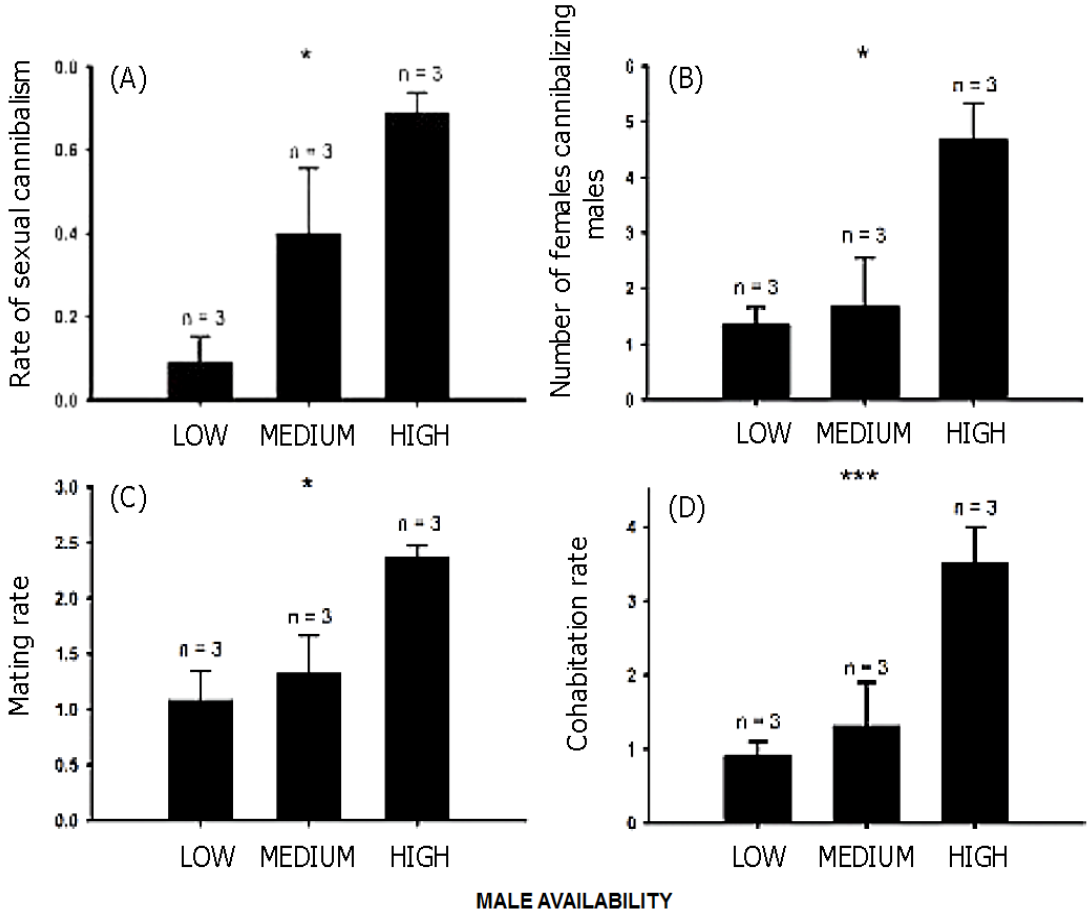

Figure 2. The effect of male availability on rates of sexual cannibalism, mating and cohabitation in female *Lycosa tarantula*. Solid bars and error bars represent means (calculated as the mean of the plot-level values of the response variables) and standard errors for the three male-density treatments, respectively. (A) Rate of sexual cannibalism–average number of cannibalistic events observed among females and averaged among plots (F2, 6 = 8.7, P= 0.017); (B) Number of cannibalistic females per plot (F2, 6 = 7.6, P = 0.02); (C) Mating rate–average number of copulations per plot (F2, 6 = 7.6, P = 0.02); and (D) Cohabitation rate–average number of males observed within 20 cm of a female burrow within each plot (F2, 6 = 25.8, P<0.001). Symbols denote significant differences among groups: *,P<0.05; *** P<0.001. More powerful tests for linear trends can be found in the text.

Field Experiment 2: Contribution of sexual cannibalism to female reproductive success

In small field plots, single isolated females that were provided a superabundance of alternative natural prey were allowed to kill a male *L.tarantula*; half of the females ("cannibalistic") were allowed to feed on the male, whereas the male was immediately removed from the jaws of the others, the "non-cannibalistic" females. Feeding on a cannibalized male enhanced several parameters directly related to reproductive success. Egg sacs of cannibalistic females were 40% heavier (GLM, $F_{1, 64} = 9.5$, $P = 0.003$, Fig. 3A), a difference that translated into a difference in the number and quality of offspring. Cannibalistic females had 30% more spiderlings per clutch (Poisson GLM, $\chi^2_1 = 4.8$; $P = 0.028$; Fig. 3B). Egg hatching success was not significantly affected by female cannibalism (GLM, $F_{1, 42} = 0.44$; $P = 0.50$), but the spiderlings of cannibalistic females were in better condition (mass/size residuals) than the offspring of non-cannibalistic females (GLM, $F_{1, 45} = 6.34$, $P = 0.015$; Fig. 3C). However, offspring size, defined as carapace width, did not differ between treatments (GLM, $F_{1, 45} = 1.10$, $P = 0.30$, Fig. 3D).

Several parameters related to the timing of reproduction also were favoured by cannibalism. Just before laying eggs, *L.tarantula* females close the mouth of their burrow with silk. The majority (80%; 28/35) of the cannibalistic females did so, whereas only 39% (13/33) of non-cannibalistic females sealed their burrows (binomial GLM, $\chi^2_1 = 12.1$; $P = 0.0006$). Cannibalistic females produced an egg sac 13 days before non-cannibalistic females (GLM, $F_{1, 65} = 11.85$, $P = 0.001$; Fig. 3E), and eggs laid by cannibalistic females developed 4 days faster than those of non-cannibalistic females (GLM, $F_{1, 37} = 8.9$, $P = 0.005$; Fig. 3F), probably due to the fact that egg sacs of non-cannibalistic females were made later in the fall, when ambient temperatures were lower. The net result of this difference in the timing of egg production was that egg sacs of cannibalistic females hatched on average 15 days earlier than those of non-cannibalistic females (GLM, $F_{1, 37} = 7.77$, $P = 0.008$; Fig. 3G).

Female survival is a major component of net reproductive rate. Mortality of females during this field experiment was high; ca. 50% died before producing an

egg sac. However, sexual cannibalism did not affect female mortality (binomial GLM, $P = 0.92$), which likely was caused by heavy rainfall. Hence effects of having fed on a male were expressed solely in the reproductive parameters of egg number, spiderling body condition, timing of egg laying, and egg developmental rate.

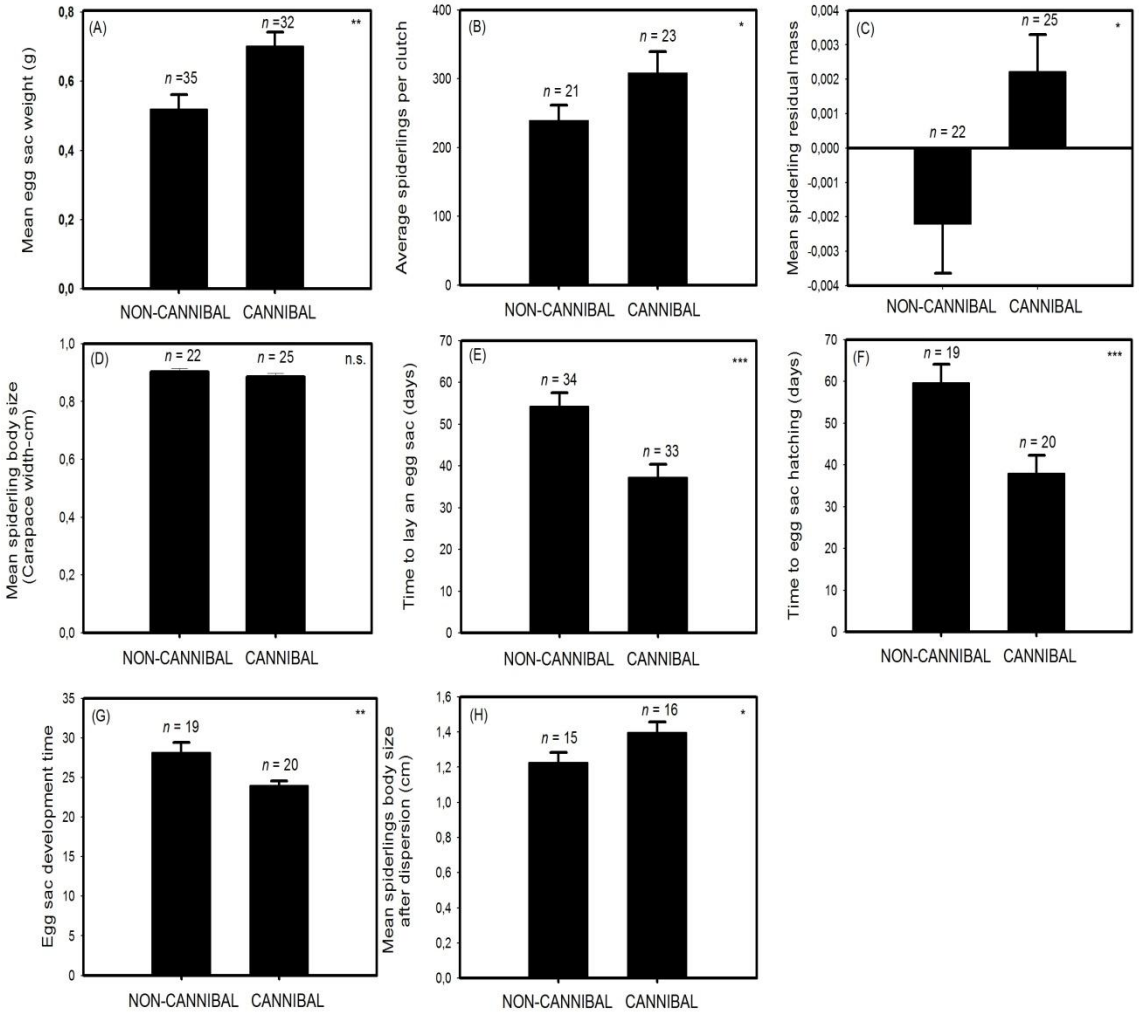

Figure 3. Effects of sexual cannibalism on several reproductive parameters of female *Lycosa tarantula*. Field Experiment 2 (A–G) and Field Experiment 3 (H). Solid bars and error bars represent means and standard errors, respectively, of (A) egg-sac mass; (B) number of spiderlings that hatched from the egg sac; (C) residual mass of spiderlings at hatching, calculated from a linear regression between the cubic root of weight and carapace width; (D) spiderling body size at hatching (carapace width); (E) time (days) elapsed between female maturation and production of the egg sac; (F) time (days) from production of the egg sac to hatching; (G) total development time (time from female maturation to egg-sac hatching); and (H) body size of spiderlings at the end of the dispersal period, which ranged from 1 to 3 months depending on the mother. Symbols denote the level of statistical significance: n.s., non-significant; *, P<0.05; **, P<0.01; ***, P<0.001.

Field Experiment 3: Survival and growth of dispersing offspring of cannibalistic and non-cannibalistic females

Subsets of recently hatched spiderlings of each female were introduced, at two different densities, into the small field plots that had housed females in Field Experiment 2. Earlier dispersal of spiderlings from cannibalistic mothers gave them more time to grow, which translated into their having a larger body size than offspring of non-cannibalistic females at the end of this experimentally delimited dispersal period (Fig. 3H). We analyzed the developmental pattern with GLM, with female (random factor) nested within the interaction spiderling density x female cannibalism (both fixed factors). Female cannibalism had a significant effect on spiderling size ($F_{1,54}$ = 5.2, P = 0.029; Fig. 3H), but there were no significant effects of either density ($F_{1,54}$ = 1.0, P = 0.321) or the density x cannibalism interaction ($F_{1,54}$ = 0.0, P = 0.850). Further analysis demonstrated that cannibalism did not directly explain the larger final size of offspring of cannibalistic females. Including the dispersal date of spiderlings as a covariate in the GLM model (covariate $F_{1,28}$ = 20.5, P = 0.0001) resulted in no effect of the cannibalism treatment on spiderling size (GLM, $F_{1,28}$ = 0.36, P = 0.555). Thus, the benefit that spiderlings obtained from their mothers having experimentally fed on a male was that of more time to grow after leaving the egg sac rather than an increase in growth rate *per se*. There were significant effects of dam (mother) on final spiderling size ($F_{27,54}$ = 3.6, P<0.0001), suggesting genetic and/or maternal effects on growth rate.

We did not find any significant effects of female cannibalism ($F_{1,25}$ = 0.3, P = 0.598), density ($F_{1,25}$ = 1.2, P = 0.281) or their interaction ($F_{1,25}$ = 0.2, P = 0.663) on spiderling survival. Release date was included as a covariate ($F_{1,25}$ = 4.5, P = 0.044) to control for the effects of time on mortality, as longer time in the enclosures should lead to increased mortality independently of any possible treatment effects.

Laboratory Experiment 1: Rates of cannibalism among offspring of cannibalistic and non-cannibalistic females

At the end of the dispersal period of Field Experiment 3, we randomly selected offspring of cannibalistic and non-cannibalistic females to test for possible advantages in spiderling-spiderling interactions that could lead to cannibalism. An

offspring of a cannibalistic female was paired in a Petri dish with an offspring of a non-cannibalistic mother. Progeny of cannibalistic females were more likely to kill and eat the other spiderling. Cannibalism occurred in 17 out of 31 Petri dishes, with the offspring of the cannibalistic female being the cannibal ca. 75% of the time ($G = 6.8$; 1 d.f.; $P = 0.009$). A second statistical analysis controlling for family effects (see Methods) was also significant (Mann-Whitney U-test, $Z = 2.03$, $P = 0.043$). The difference in size between spiderlings (Percentage Difference in Size, PDS: [{size_large–size_small}/size_small] *100 (Moya-Laraño & Wise 2000) significantly explained whether or not cannibalism would occur (binomial GLM, $\chi^2_1 = 21.6$; $P<0.0001$), suggesting that the progeny of cannibalistic females had an advantage solely because they were larger and not because they benefitted in any other way (e.g. greater strength) from being the offspring of a mother who was experimentally allowed to cannibalize a male.

Discussion

Our experiments strongly suggest that pre-copulatory sexual cannibalism occurs at a substantially high rate in natural populations of *L.tarantula*, and that this behaviour is an evolved female adaptation to a limited supply of high-quality prey. Below we evaluate the evidence supporting these conclusions and discuss several implications of our findings.

Commonness of pre-copulatory cannibalism by *L. tarantula* females in nature

The rate of pre-copulatory sexual cannibalism by females in *L.tarantula* populations is likely quite high, as approximately a third of the females in Field Experiment 1 were observed killing and consuming a potential mate instead of copulating with him. In fact, and perhaps somewhat surprisingly, less than 5% of cannibalism by females was post-copulatory. This experiment was conducted under conditions very close to natural: female burrows were spread throughout the plots at a natural density, males were free to roam, and prey density and composition were maintained close to normal by the trapping protocol at plot boundaries. The major factor complicating the extrapolation of this

cannibalism rate to a completely non-manipulated natural population is the variation in male densities produced by our intentional alteration of sex ratios in the plots, and by the high mortality of males during the experiment, probably due to bird predation, as these were the only predators that were not excluded (see Methods). In natural populations of *L.tarantula* the sex ratio varies throughout the mating season as male mortality from predation and cannibalism causes their numbers to decline more rapidly than females (Moya-Laraño et al. 2003a,b). It is also likely that the seasonal changes in sex ratio may vary from one area to another, depending upon differences between localities in predation pressure on males. However, local male availability around a female burrow is not only influenced by the population sex ratio, but also by the behaviour of males, who show great variation in moving rates in search of females (data collected during this study and to be published elsewhere). The female should respond to variation in local male availability, since this may be the only estimate of male availability that she can assess.

Comparison with other studies of *L.tarantula* supports the conclusion that the range in local male availability across our treatments was within the natural range. In Field Experiment 1 the number of different males observed encountering each female ranged from 1.0 to 3.6 across the male-density treatments, which we conclude likely falls within the natural range for two reasons. First, in a previous study of this population in Almería, employing a comparable sampling effort, we found that at the end of the mating season, when males are a scarce resource (Moya-Laraño et al. 2003a), the number of males observed visiting each female was 1.3±0.1—a number equal to that observed in the Medium male-availability treatment in the current study (1.3±0.4). Secondly, data from another population (Moya-Laraño et al. 2003b), in which sampling effort was ¼ that of the present study (females were only visited once every other night during the mating season), showed that across the entire season each female was visited by at least 1.9±1.4 males. Conservatively assuming that we had missed half of the visitations in that study leads to an estimated visitation rate of ~3.8 different males visiting each female on average, which is very close to the visitation rate observed in the High male-availability treatment in the present study (3.5±0.5). Thus, our male-

density manipulations yielded encounter rates that are within the range found in completely natural, non-manipulated populations.

Evidence that pre-copulatory cannibalism in *L. tarantula* is adaptive

How could high rates of pre-copulatory cannibalism be adaptive–how can natural selection favour the killing of a mate by a female before she has gotten his sperm? Arnqvist and Henriksson (1997) proposed that under conditions in which the adult female is not food-limited, the "aggressive spillover" hypothesis could explain the evolution of pre-mating sexual cannibalism, which would be the consequence of aggressive predatory behaviour that is adaptive at an earlier life stage and that continues to be expressed in the mature female, even though it does not increase female fitness (in comparison to females who could suppress the expression of this genetically determined behaviour) (Arnqvist & Henriksson 1997). Four facts argue strongly against the spillover hypothesis as the major explanation for the evolution of pre-copulatory sexual cannibalism in *L.tarantula*: (1) male *L.tarantula* are high-quality prey whose consumption improves several parameters of reproductive output (this study); (2) negative effects of strong food limitation experienced by juvenile female *L.tarantula* appear to be offset by cannibalizing mature males (Moya-Laraño et al. 2003b); (3) in the current study most *L.tarantula* females who cannibalized males had already mated, and hence already had received sperm (although the possibility of a fitness cost remains if additional matings increase fecundity or improve fitness by increasing genetic diversity of the offspring); only 8% of females in Field Experiment 1 and 9% in Field Experiment 2 killed a male as a virgin; (4) females are more likely to attack males if their availability is higher (current study); a greater availability of males increases the probability that a female who has cannibalized a potential mate will encounter another one before she lays eggs. Taken together, the above findings strongly support the adaptive foraging hypothesis (Newman & Elgar 1991) as an explanation for the evolution of pre-copulatory sexual cannibalism by female *L.tarantula*.

However, in our results some element of "aggressive spillover" cannot be ruled out completely, because by killing males, some female *L.tarantula* risk

remaining unmated. In Field Experiment 1, three out of the six virgin females who killed an approaching male remained unmated because they were in the Low male-availability treatment. This treatment may mimic what happens at the very end of the mating season, when males are scarce and some females remain unmated (Moya-Laraño et al. 2003a). Early-maturing females, who have more time to find a mate and are likely food-limited, should gain more by killing the first approaching male. However, in the current study there was no relationship between the tendency to cannibalize as a virgin and the timing of maturation, indicating that virgin females who attacked males were not early-maturing females. Therefore, some of the tendency towards sexual cannibalism by virgins may be misdirected aggression, spillover from (1) aggressive behaviour related to foraging for prey, which occurs at night when males are near the burrow mouth (Moya-Laraño et al. 2004); and (2) cannibalistic behaviour directed at other mature females, which is a component of territorial defense (Moya-Laraño et al. 2002a). Evidence suggests strongly, however, that any spillover effect, if present, is a minor component of *L.tarantula* sexual cannibalism, which appears to be primarily an adaptive foraging strategy.

In *L.tarantula* pre-copulatory cannibalism appears to be adaptive behaviour that has evolved to overcome negative effects of food limitation on female reproductive rate. Females that had cannibalized a single male produced more offspring with a better body condition. These females also laid their egg sacs sooner in the season, which promoted more rapid development because of warmer temperatures. A similar pattern was found in the wolf spider *Pardosa milvina* in which females fed high-quality diets in the laboratory produced eggs sacs more rapidly than females reared on a low-quality diet (Wilder & Rypstra 2008). The result is that earlier dispersal of the spiderlings of cannibalistic females allowed them to grow to a larger size by the end of the season. These effects of cannibalism were directly due to an alleviation of food limitation, and not due to any possible genetic correlation between cannibalistic behavior and aggressive foraging behavior for prey, because in Field Experiment 2 females in both treatments had killed a male. By permitting only half of these females, selected at random, to feed completely on the male that we offered to them, we ruled out any possibility that

the benefit of a male as a meal to the cannibalistic female was a spurious artefact of the fact that females who tend to be more cannibalistic may be more aggressive and thereby more successful in capturing other prey (Elgar & Schneider 2004; Arnqvist & Henriksson 1997). This benefit of cannibalism to the female is consistent with the fact that males are several times larger than alternative prey (Moya-Laraño et al. 2002a), which makes a single male a more valuable prey simply in terms of calorie content.

The male appears to be a valuable source of prey not only because it is a larger bundle of calories than the alternative prey available to *L.tarantula*. In Field Experiment 2 the females had available to them a superabundance of prey species found in nature, yet consuming a single male dramatically improved reproductive output. Since calories are substitutable for a generalist predator (all other things being equal, such as prey defensive behaviors, digestibility of the prey tissues, etc.), it must not only be the calories contained within males that are important for female *L.tarantula*. Other evidence supports this conclusion. For example, cannibalistic females were more likely to close their burrows with silk. The quality of the silk produced by spiders closely depends on the quality of the prey in the diet (Craig et al. 2000), suggesting that females perhaps alleviate nitrogen limitation by feeding on males. Nitrogen limitation of female *L.tarantula* in a different population is suggested by indirect measurements of nutrient content in females that had been collected from the field as ante-penultimate instars (Moya-Laraño et al. 2008). Additional evidence for male *L.tarantula* being high-quality prey comes from the fact that most alternative prey for *L.tarantula* females are detritivores (Moya-Laraño et al. 2002a), which in aquatic food webs have higher C:N ratios than arthropod predators (Cross et al. 2003, 2007). Thus, sexual cannibalism in *L.tarantula*, in addition to providing a large packet of easily extractable calories, may secure the additional benefit of redressing nutritional imbalance experienced by females, which seems particularly crucial during the egg-ripening stage (Moya-Laraño et al. 2008). It would be worthwhile to know whether or not female *L.tarantula*, in addition to attacking males at rates that reflect the extent to which they have experienced a scarcity of natural prey (Moya-Laraño et al. 2003b), are more likely to attack males if they are suffering a nutritional imbalance, as it has been shown for arthropod predators exposed to

heterospecific prey (Mayntz et al. 2005). Nutritionally unbalanced wolf spiders have been shown to be less efficient at feeding on prey other than conspecifics (Mayntz & Toft 2006). This phenomenon may explain why, in our experiment, the females that had not fed on a male laid smaller egg sacs despite having large amounts of alternative prey in the enclosures (see Methods). Therefore, redressing nutritional imbalance by feeding on a male may improve how well females process other prey. Experiments with wolf spiders suggest that food limitation may lead to enzyme limitation that in turn constrains foraging efficiency (Samu 1993).

Female flexibility in cannibalistic tendencies suggests that pre-copulatory cannibalism by *L.tarantula* is primarily an adaptive foraging behaviour, in which females weigh the benefits of males as sperm donors or prey. Despite the fact a male is an excellent food resource, females generally behave adaptively towards approaching males. Several results support this interpretation of flexible female behaviour towards males. First, few virgin females (8% in Field Experiment 1, 9% in Field Experiment 2) killed approaching males. The proportion of females that killed approaching males rose to 25% once females had secured sperm for egg production (Field Experiment 1), a pattern found in other studies (Elgar 1998; Johnson 2001; Herberstein et al. 2002; Erez et al. 2005). Second, females tend to kill males at a higher rate as more males are available (Field Experiment 1). This difference was statistically significant even after controlling for the female *per capita* encounter rate with males. Thus, females were not preying on males at a higher rate merely because the encounter rate between females (predators) and males (prey) was higher in plots with higher male availability. This result strongly suggests that a female's decision to kill a potential mate was based at least partly on her assessment of male availability. A laboratory experiment with the fishing spider *Dolomedes triton* (Johnson 2005), in which females were experimentally induced to assess the environment as rich or poor in males, found similar results. However, Johnson's laboratory experiment (Johnson 2005) is not easily interpretable, as its design did not control whether females assessed males as such, or whether females were mistaking males as highly mobile prey. Although Johnson used juvenile *D. triton* presumably to control for the possibility that females were

mistaking males for potential prey, the mobility of juvenile *D. triton* is much less than that of females (Kreiter & Wise 1996) , which in turn, as in most spiders, must be lower than that of males (Moya-Laraño et al. 2002b; Foellmer & Moya-Laraño 2007). Our field manipulations of actual male availability eliminated alternative explanations for the observed pattern, thereby providing strong support for the hypothesis that females behave adaptively towards approaching males, being more likely to attack once they have assessed the environment to have a high availability of males.

Fitness benefits to the cannibalistic female via progeny traits

Surprisingly, the better body condition of the offspring of cannibalistic females did not translate into any measurable fitness benefits after spiderling dispersal (Field Experiment 3). This apparent paradox may be explained by the fact that in nature not all spiderlings disperse at once, as we experimentally induced. In fact, for this species there appear to be two dispersal peaks of siblings: one before and another after the winter (Humphreys 1983; Parellada 1998; Moya-Laraño & Cabeza 2003). Perhaps spiderlings in better condition have less of an immediate need for food and therefore tend to remain with their mothers during winter. Indeed, the relative benefits of a better body condition may depend upon the net fitness benefit of dispersing before or after the winter, which may change from year to year depending on variation in weather conditions (Humphreys 1983; Moya-Laraño & Cabeza 2003).

The male perspective

Sexual cannibalism occurs very rarely after mating in *L.tarantula*, as we observed only one case of post-mating sexual cannibalism. Therefore, most cannibalized males are eaten by females with whom they have not mated, which means that the selective benefit of sexual cannibalism to most males is zero. Hence, female cannibalistic behaviour should impose a strong selective pressure on males to evolve counter-adaptations to avoid female attacks. Previous research on *L.tarantula* suggests that males do not approach females randomly, but instead, approach females at times of day when predation risk is lowest (Moya-Laraño et al.

2004) and/or they preferentially approach females that present a lower predation risk (Moya-Laraño et al. 2003a). Females, on the other hand, apparently have been selected to behave adaptively towards males. It remains to be investigated whether this female adaptive behaviour (i.e., attacking males only after ensuring sperm) has evolved from selection imposed by males that preferentially approach non-aggressive females or because high male mortality during the mating season (Vollrath & Parker 1992; Moya-Laraño et al. 2002b; Foellmer & Moya-Laraño 2007) entails a high risk of remaining unmated for females in natural populations.

Conclusions

The results of our research are particularly relevant to understanding the ecology and evolution of sexual cannibalism because (1) the data were gathered in field experiments conducted under natural conditions; (2) sexual cannibalism (Elgar 1992) and cannibalism in general (Wise, 2006) are widespread among spiders; and (3) spiders are abundant and ubiquitous in terrestrial systems (Wise 1993). Data on sexual cannibalism were obtained under natural rates of encounter between males and females, with the same opportunities for males to escape female attacks as occur in nature. The experiments revealed a high incidence of sexual cannibalism in a natural population of *L.tarantula*, and demonstrated that a diet including a single male is much better than a diet consisting only of alternative natural prey, strongly suggesting that sexual cannibalism may help females to alleviate calorie and nutrient limitation. Thus, in *L.tarantula* pre-copulatory sexual cannibalism is an evolved, adaptive foraging strategy.

Acknowledgments

We thank Lupe Corcobado, David García, Alejandro Moreno, Nereida Melguizo and Virginia Pérez for helping in the field. We also thank Alfredo Durán and Ramón Ordiales for logistical advice. We are indebted to Isabel Cueva and Matthias Boer for letting us use their land for the experiments.

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MANUSCRITO II

Does Female Personality Determine Mate Choice Through Sexual Cannibalism?

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Publicado en:

Ethology (2014) 120(3) 238-248

Resumen

Las personalidades animales, definidas como diferencias comportamentales entre los individuos que son consistentes entre contextos, pueden contribuir a generar diferencias en la elección de pareja. Sin embargo, hay escasa evidencia de que exista esta conexión. El canibalismo sexual pre-cópula puede ser un síndrome comportamental (una personalidad sub-óptima), en la que la agresión adaptativa de la hembra hacia sus presas heterospecificas se manifiesta con la agresión no adaptativa hacia los machos que las cortejan, que es independiente del estado emparejador o alimenticio de la hembra (hipótesis de 'spillover' agresivo, ASH). Por otro lado, el canibalismo sexual puede ser una forma de elección de pareja por la que las hembras matan selectivamente o se aparean con los machos según su fenotipo. Introducimos la hipótesis de que las hembras más agresivas de una población no solo atacarán con mayor frecuencia a los machos, sino que también tenderán a ejercer presiones de selección sexual sobre los machos a través del canibalismo sexual relativamente bajas. Asumiendo que en un experimento de campo de "jardín común" en el que se alimenta a las hembras *ad libitum,* la tasa de engorde de la hembra refleja su voracidad o agresividad, este estudio muestra que en la araña lobo caníbal *Lycosa hispanica* (anteriormente *L. tarantula*) la voracidad de las hembras hacia presas heterospecíficas predice su tendencia al canibalismo sexual. Las hembras que no se habían apareado y engordaban más eran más caníbales, y atacaban a los machos independientemente del fenotipo de éstos. En las hembras menos voraces, en cambio, la tendencia al canibalismo era más débil, además de que éste era selectivo, ya que las hembras tendían a atacar a los machos en peor condición corporal, mientras que preferían aparearse con los machos con una condición superior. Nuestros resultados demuestran que las hembras tienen diferentes fenotipos agresivos (tasas de crecimiento) y éstos tienden a imponer selección diferencial sobre la condición del macho, lo que apoyaría la hipótesis de que la agresividad de la hembra interfiere con la selección sexual a través el canibalismo sexual.

Palabras clave: *síndromes comportamentales, audacia, Lycosa hispanica, canibalismo sexual, selección sexual, agresión spillover*

Abstract

Animal personalities (e.g. consistent across-context behavioural differences between individuals) can lead to differences in mate choice. However, evidence for this link remains limited. Pre-mating sexual cannibalism can be a behavioural syndrome (i.e. a suboptimal personality) in which adaptive female aggression towards heterospecific prey spills over on non-adaptive aggression towards courting males, independently of the female mating or feeding status (i.e. the 'aggressive spillover hypothesis', ASH). On the other hand, sexual cannibalism can also be a form of mate choice by which females selectively kill or mate with males depending on the male phenotype. We introduce the hypothesis that the most aggressive females in the population will not only attack males more frequently, but will be less likely to impose sexual selection on males through sexual cannibalism. Assuming that in a field common garden experiment in which females were fed ad libitum the rate of weight gain by a female may reflect her voracity or aggressiveness, we show that in the cannibalistic burrowing wolf spider Lycosa hispanica (formerly L. tarantula), voracity towards heterospecific prey predicts a female's tendency towards sexual cannibalism. Unmated females with higher weight gains were more cannibalistic and attacked males regardless of the male phenotype. On the other hand, females that were less voracious tended to be less cannibalistic, and when they did kill a male, they were selective, killing males in poorer condition and mating with those in better condition. Our results demonstrate that females with different phenotypes (growth rates) differently imposed selection on male condition, tentatively supporting the hypothesis that female aggression levels can spill over on sexual selection through sexual cannibalism.

Keywords: *behavioural syndromes, boldness, Lycosa hispanica, sexual cannibalism, sexual selection, spillover aggression*

Introduction

Behavioural syndromes are suites of behaviours that are correlated across a variety of contexts. The key point is that some of these contexts may enhance individual fitness while others may be detrimental for individual fitness, leading to a suboptimal net effect (Sih et al. 2004a,b; Bell 2007). This may explain why non-adaptive behaviours are maintained in populations despite their manifest biological inefficiency (Sih et al. 2003; Johnson & Sih 2005; reviewed in Bell 2007). One of these contexts may be mate choice occurring during sexual encounters, and it has been suggested that female personality may affect how females exert sexual selection on male traits. This last topic, however, remains little explored (reviewed in Schuett et al. 2010).

A classic example of behavioural syndrome is that of pre-mating sexual cannibalism by spillover aggression of females (i.e., the "Aggressive Spillover Hypothesis", ASH, Arnqvist & Henriksson 1997; Sih et al. 2004a,b; see Kralj-Fišer et al. 2013 for a review). In sexually cannibalistic species a female may kill a courting male, before, after or during copulation (Elgar 1992), and it is this timing that may crucial for the costs incurred by females. If males are a limiting resource as sperm donors (Arnqvist & Henriksson 1997; Moya-Laraño et al. 2003a) and attacks occur before a female has mated the female risk of remaining unmated should be relatively higher. The ASH states that highly aggressive females, which would attack heterospecific prey and display therefore higher growth rates and subsequent enhanced fecundities, will also attack males indiscriminately (i.e., regardless of the female feeding or mating status). The latter behaviour would be maintained in populations from fecundity selection acting on females (Arnqvist & Henriksson 1997). This necessarily involves a genetic quantitative basis for aggression, as it has been demonstrated in some spider species (Riechert and Maynard-Smith 1989; Riechert & Hedrick 1993; Kralj-Fišer & Schneider 2012). The ASH finds support on two studies in the sexually-cannibalistic fishing spider *Dolomedes triton* (Johnson & Sih 2005; 2007). Recently, however, it has been argued that support for this hypothesis is not very strong, and that further

research is needed (Kralj-Fišer et al. 2013; but see Johnson 20013 and Pruitt & Keiser 2013).

Behavioural syndromes have also been recently expanded to incorporate behavioural reaction norms by which animals with certain personalities can respond flexibly and consistently when the context changes in a similar manner (Dingemanse et al. 2009). For instance, in spiders, females may attack males at a higher frequency when males are more abundant (Rabaneda-Bueno et al. 2008), when females are hungrier (Andrade 1998; Moya-Laraño et al. 2003c) or after females have already mated at least once (Johnson 2001; Rabaneda-Bueno et al. 2008). This plastic capacity exhibited by females have the potential to determine how sexual cannibalism acts as a form of mate choice on male morphology (Persons & Uetz 2005; see Prenter et al. 2006 for a review on sexual cannibalism as a form of mate choice), as females may decide to mate with some males or attack and consume others. Interestingly, a recent study in *Nephilengys livida* (Araneae: Nephilidae) concluded that the quality of spider males may be more relevant to explain female cannibalistic behaviour than female aggressive (spillover) personality itself (Kralj-Fišer et al. 2012). Furthermore, the ASH implicitly involves that maintained female aggression across contexts could also imply that the most aggressive females in the population would kill males without discriminating among male phenotypes. Therefore, only the least aggressive females in the population (e.g., those with relatively low growth rates) would be able to exert mate choice.

In a field experiment, we confined 99 males and 80 females of the Iberian tarantula *Lycosa hispanica* (formerly *L. tarantula* for the Iberian Peninsula - Planas et al. 2013) in enclosures. We studied the occurrence of mating and pre-mating cannibalism of females with no mating history (i.e., virgin), and investigated the link of these behaviours to a proxy of their voracity against heterospecific prey, the rate of weight gain prior to the first encounter with a male when the female was fed *ad libitum*. We used this proxy to test the novel hypothesis that highly voracious feeding females, if they spill aggression on sexual cannibalism, will be less discriminating against approaching males. To test this hypothesis we tested 3 predictions in steps: (1) the main prediction of the ASH: Are the most voracious

females in the population more likely to attack and kill a male? (2) the sexual selection hypothesis of mate choice (Prenter et al. 2006): Are females selection agents on male phenotypes, mating with males within a particular trait range and killing and consuming males out of this range?, and finally (3) Are the most voracious females less discriminating, attacking males regardless of the male phenotype?

Methods

Study Species

The Iberian tarantula, *L. hispanica,* is a food limited, territorial and burrowing wolf spider of relatively low sexual size dimorphism (Fernández-Montraveta & Moya-Laraño 2007; Foellmer & Moya-Laraño 2007), and which has been shown to be a well suited species for the study of premating sexual cannibalism. In *L. hispanica* the majority of sexual cannibalism occurs before mating and mostly by females that have already mated (Moya-Laraño et al. 2002; 2003a; Rabaneda-Bueno et al. 2008). Courtship and mating patterns have been described somewhere else (Orta-Ocaña et al. 1996; Moya-Laraño et al. 2003a). In captivity, males raise their legs for courtship when they sense the presence of the female and use palpal drumming on the female turret.

Experimental procedures

A part of this experiment aimed to document the benefits of sexual cannibalism to females (results and detailed experimental procedures can be found in Rabaneda-Bueno et al. 2008) and the data presented here only cover the array of female reactions towards males until their first mating. Subadult females (N=80) were captured from a natural population of a nearby area to the Cabo de Gata-Níjar Natural Park (Almeria, South Spain, Moya-Laraño et al. 2002; 2003a; 2004). Each female was individually placed into an artificial burrow inside a 1x1x0.3-m field enclosure and was fed natural prey *ad libitum*, most of which were darkling beetles (Tenebrionidae) and woodlice (Isopoda), consistently supplied

throughout the experiment. Mating occurs inside the burrow and close to its entrance, thus easing the sampling of mating events (e.g. Moya-Laraño et al. 2003a; Rabaneda-Bueno et al. 2008). Upon presentation of males a few of the females either killed the male or refused to mate with him, in which case they were presented additional males until a complete copula was achieved. Due to the relatively small size of the mating cages (see below), males could not escape female attacks which allowed identifying aggressive encounters unequivocally. Despite the male inability to elicit an escape response our observations minimized cannibalistic effects on the male population because they took place at the time of the day when attacks are at a minimum (Moya-Laraño et al. 2004) and also knowing in advance that virgin females are less prone to cannibalism (Rabaneda-Bueno et al. 2008). Hence, this procedure reduced the risk incurred by males and the artificial bias towards cannibalism, which would have created unnecessary damage upon males. We measured the carapace and abdomen widths (nearest 0.01 mm) of males and females, and all individuals were weighed (nearest 0.01 g) at maturation and before running each mating trial. Since measurements were performed under a dissection microscope, we estimated intra- and inter-observer repeatability to be >0.95. We used carapace width (CW) as the estimate of (structural) body size. Instead of including body mass in the regression model to estimate body condition (Moya-Laraño et al. 2008), we calculated body condition as the residuals of a regression of cubic root body mass on CW. This procedure allowed estimating a true statistical interaction between (residual) body condition and body size (CW); i.e., the interaction term was not confounded by the share of body mass between the abdomen and CW.

Inducing male-female encounters and recording behavioural outcomes

On average, 3 weeks after a female had moulted to adulthood we introduced an adult male –which had previously been randomly assigned to one of the 80 female burrows-, into a 20 x 20 x 10-cm metal cage placed on top of the burrow entrance. Considering that normal cohabitation distances during the day are ca. 3cm (Moya-Laraño et al. 2004), these small cages were enough in size to let the male move around the female burrow, but they did not prevent male capture by an attacking female. Female receptivity, on the other hand, was not affected by the

time since maturation, as we found no significant effects of this variable on any of the models in which it was included or on their final outcomes (not shown). Each experimental day, we released a different male in each of 8 female burrows. Mating trials (the male release into the enclosures) started between 8:00 and 9:00 am, which lays within the time window when mating frequency is highest in this species (Moya-Laraño et al. 2003a, Moya-Laraño et al. 2004, Rabaneda-Bueno et al. 2008), To document behavioural outcomes in the enclosures, we visited the burrows at 10-min time intervals during the first 2 hours since the start of the trials and every 30 minutes thereafter until all active mating couples had concluded (max. 15 hours). Each male was used only once in a single trial and then released back into the field. Some of the males released achieved successful mating while others failed to mate. In total, we released 99 males of which, 13 died from cannibalism by 9 females. Because sexual cannibalism in *L. hispanica* occurs almost exclusively before mating (Rabaneda-Bueno et al. 2008), and females remain inactive during the day unless a male court and try to mate with them (Moya-Laraño et al. 2004), cannibalism occurred as a product of the active male attempt to court the female and enter the burrow. During the trials, some males did not engage in active response towards females and remained motionless outside the burrow (12 out of 99 males froze in front of 10 females). In these cases, after a period of 2 hours of male inactivity, males were removed from the enclosure. During this stand-still reaction in front of the burrow's mouth ("freezing"), neither cannibalism nor mating were recorded (passive interaction), and therefore, in terms of energy and time invested, its effects on male fitness ranged between those of mating and cannibalistic interactions. Three possible (mutually exclusive) outcomes were hence derived from the mating trials: mating, freezing and cannibalism, which, for statistical analyses (see below) were ranked from highest to lowest effects on fitness.

Estimating the female rate of weight gain as a potential proxy of voracity

The prediction of the spillover hypothesis in the context of this study implies that if voracity on heterospecific prey by virgin females predicts whether a female will attack a male this will be evidence that aggression on heterospecific prey spills over on adult cannibalism against courting males. Since for logistic

reasons we failed to monitor female feeding activity in our experiment we used a proxy of voracity given by the growth achieved by virgin adult females under an *ad libitum* feeding regime. Voracity was therefore estimated as the daily rate of weight gain during the time elapsed between the date of maturation and the date when a female was first presented a male. This last estimate is important in the context of the spillover hypothesis. In the present study, in which conspecific aggression was measured with 100% confidence and every attacked male ended up cannibalised (see above), we assumed that a single male cannibalised by a female should reflect high aggresion levels in a context other than conventional predation on heterospecific prey. Therefore, albeit suboptimal, we had the two necessary contexts (voracity before mating and aggression during mating) to test the ASH. However, since the rates of weight gain can also be explained by several related traits (e.g., assimilation efficiency, aggression, hunting ability and/or boldness) in addition than by the environment, we conservatively disentangled the potential sources of variation in a causal diagram explaining the rationale used in the present study (Figure 1, following Biro and Stamps 2008; see also Moya-Laraño 2011; Moya-Laraño et al. 2012).

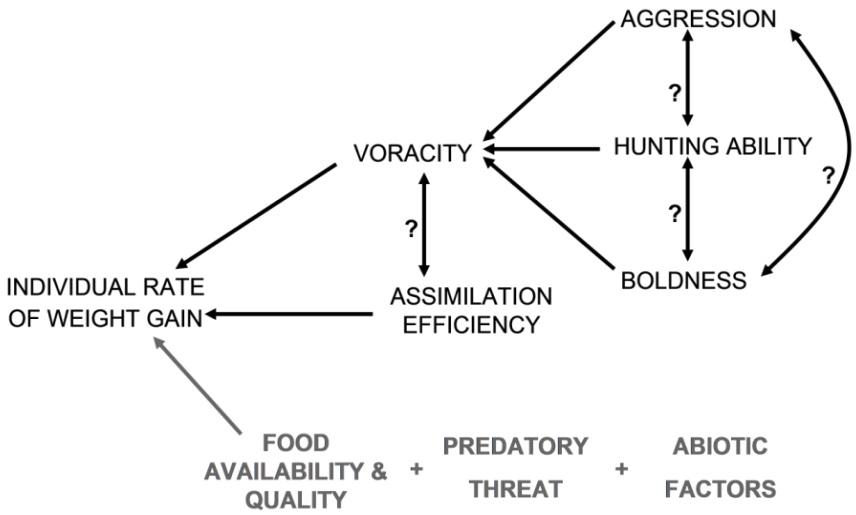

Figure 1. Drivers of individual growth rate in a generalist predator. A combination of behavioural and physiological traits (black text and arrows), which may be or may not be correlated with morphological traits, and which in turn may be correlated with each other, plus environmental variability (food availability and quality, predation threat and abiotic factors, grey text and arrows), determines interindividual differences in rates of weight gain. If variability in assimilation efficiency (i.e. how much of the ingested food is converted into own mass) is negligible as compared to variability in voracity; environmental conditions are kept constant across individuals (common garden), variability in individual rates of weight gain likely reflect variability in voracity, which in turn may be the consequence of a mixture of other traits. Question marks denote potential correlations and trade-offs between traits (Biro & Stamps 2008; Moya-Laraño 2011; Moya-Laraño et al. 2012).

Statistical Analyses

Four females were dropped from the analysis (final N=76) either because they died during the experiment or because they had been inadvertently collected as antepenultimates and did not mature in time to be included in the experiment. We analysed the data using Proportional Odds Generalized Linear Mixed Models (POGLMM) for Ordinal Responses (*polr* function in library *MASS* of R, or *clmm* in library *ordinal* if random effects were included in the model– R development core team 2010; Christensen 2010). This type of GLMM is especially suited for the nature of our dependent variable, which was ordinal (ordered categorical) in nature. This is because we ranked the three mutually exclusive outcomes (mating, freezing or cannibalism) from highest to lowest fitness effects on males: mating – rank 3, freezing – rank 2, cannibalism – rank 1.

Using this ranking the sign of the estimates relating the response variable to the predictors could be interpreted in terms of the probability of achieving an outcome that increased or decreased male fitness. Positive estimates were associated with an increase in male fitness as the values for male or female traits increased, whereas negative estimates meant decreasing male fitness with an increase in trait value. Another way to interpret the results is that positive estimates meant that a trait was positively associated with the probability of mating and negative estimates that a trait was positively associated with the probability of cannibalism. To test for the sensitivity of the conclusions to the modelling approach, we re-analysed these data through additional models (binomial for pairs of first female responses, multinomial logit for non-ranked multinomial responses and lastly Generalised Estimating Equations –GEE- considering the autoregressive nature of the response variable), using the R libraries *lme4* (Bates & Maechler 2010), *mlogit* (Croissant 2010) or *geepack* (Højsgaard et al. 2005) respectively. Since growth rates were measured for a variable number of days for each female individual (range 3-38, see "Inducing male female encounters" above) and the number of days elapsed affected growth rates ($r=0.52$, $p<0.001$), we also ran models including the number of days used for the estimation of growth rates. In all cases the results were always qualitatively consistent (not shown).

To test if the female rate of weight gain prior to a first encounter with a male could explain their tendency to copula or cannibalism, independently of her body size and condition, we fitted a series of POGLMM candidate models and chose the one with the lowest Bayesian Information Criterion (BIC) value. This criterion performs better than the alternative Akaike's Information Criterion (AIC) (Burnham & Anderson 2002) when one wants to minimise the number of parameters in the final model (Quinn & Keough 2002), We then checked if our estimate of female voracity was included in the final model, and if its effect was significant and in the predicted direction of a behavioural syndrome. As some females were exposed to more than a male before they mated, we included female identity as a random factor in all models.

Secondly, we tested the hypothesis that sexual cannibalism is a form of mate choice, by building a series of POGLM models in which two male morphological traits (carapace width and residual body mass; i.e. body condition) and their quadratic and interaction terms, would serve to test for directional, stabilising, disruptive and correlational selection acting on male morphology (e.g. Fernández-Montraveta & Moya-Laraño 2007). Again, we used the BIC method to select the most parsimonious model with the minimum number of predictors.

Lastly, we searched for a link between female voracity and selection on male phenotypes through sexual cannibalism, by fitting a POGLMM model including female identity as a random factor, and searching for models including an interaction between female growth rate and male phenotype on the rank variable (cannibalism, freezing, mating). Using BIC in our model selection approach allowed achieving maximum power by testing a single interaction term for this third prediction –note that as the number of predictors and their interactions increases statistical power decreases. To visualise if a significant interaction in the above model follows the prediction that the most aggressive females are less selective on male phenotypes, we displayed the results of the interaction using an interaction plot for POGLMs (library *effects* in R – Fox 2003).

Results

Are the most voracious females in the population more likely to attack and kill a male?

The female rate of weight gain was a good predictor of the female tendency to cannibalise or to mate with a male. The model with the lowest (BIC=154, Table 1) included only the female rate of weight gain (estimate=-71.3, Z=-2.66, *P*=0.008). Because of how the response variable was coded (mating – rank 3, freezing – rank 2, cannibalism – rank 1), a negative estimate indicates that a higher rate of weight gain increases the chances of killing instead of mating with an approaching male. In fact, the female rate of weight gain was the only trait significant across models, being significant and negative in 4 out of 5 models in which this variable was included. The correlation between weight gain and body size and weight gain and condition was very low (both r∼-0.1; p>0.52), thus likely not interfering with model selection.

Are females selection agents on male phenotypes, mating with males within a particular trait range and killing and consuming males out of this range?

Females tended to impose selection on male body condition, tending to mate with males in good condition and killing males in poor condition. The model which best explained selection upon male traits was that including male body condition only (BIC=155, Table 1) (estimate=19.0, Z=2.15, P=0.03). There was no evidence for stabilising or disruptive selection on this trait (quadratic terms were not significant). Indeed, the linear trend for male body condition was the only significant trait across models (3 out of 4). We could not test saturated models (with all the interactions and quadratic terms) because most likely due to the relative few cases of cannibalism and freezing, these models produced marginal probabilities or 0 or 1, rendering then unsolvable. Thus, males in better condition were preferred as mates rather than as meals.

		Regression coefficient of variable in model				
BIC	Δ BIC	Female CW	Female condition	Rate of weight gain	CW x Rate	CW x Cond
a) Female traits affecting male fitness						
154	0			71.3**		
156	2	0.9		80.9**		
157	3					
158	4		3	71.0**		
160	6	0.59				
160	6	1.0		262	18.7	
161	7	0.89	1.23	80.5**		
161	7		4.6			
165	11	0.59	4.42			
166	12	0.59	420.3			43.7

		Regression coefficient of variable in model				
BIC	Δ BIC	Male CW	Male condition	CW x Cond	$Cond^2$	CW^2
b) Selection on males						
155	0		19.0*			
156	1					
158	3	0.6	19.5*			
158	3	0.4				
159	4		17.4*		152.7	
161	6	12.6				0.7
161	6	0.5	142.6	13.2		

Table 1. Model selection approach to uncover (a) female traits or combinations of traits that affect male fitness and (b) selection on male traits. Tests are proportional odds generalised linear models on the outcome of the male–female interactions (ordinal variable: cannibalism (1), freezing (2) and mating (2)). Models were ranked from more to less parsimonious according to Bayesian information criterion (BIC); ΔBIC = difference in BIC value relative to the best ranked model (Model 1). Saturated models (with more interactions and quadratic terms) could not be estimated because perfect (0 or 1) marginal probabilities were reached.

Are the most voracious females less discriminating, attacking males regardless of the male phenotype?

As predicted, the most voracious females tended to be less selective, killing males regardless of the male condition. In contrast, the females that gained weight at a lower rate prior to being offered a male, were highly selective, tending to mate with males of intermediate to good condition and killing males in worse condition (Female growth rate, estimate=-112.4, Z=-3.33, P<0.001; Residual male mass, estimate=49.8, Z=3.27, P=0.001, Interaction, estimate=-2031, Z=-2.37, P=0.018; Figure 2). There was also a clear tendency for males to freeze at a higher rate when approaching the most voracious females (Figure 2).

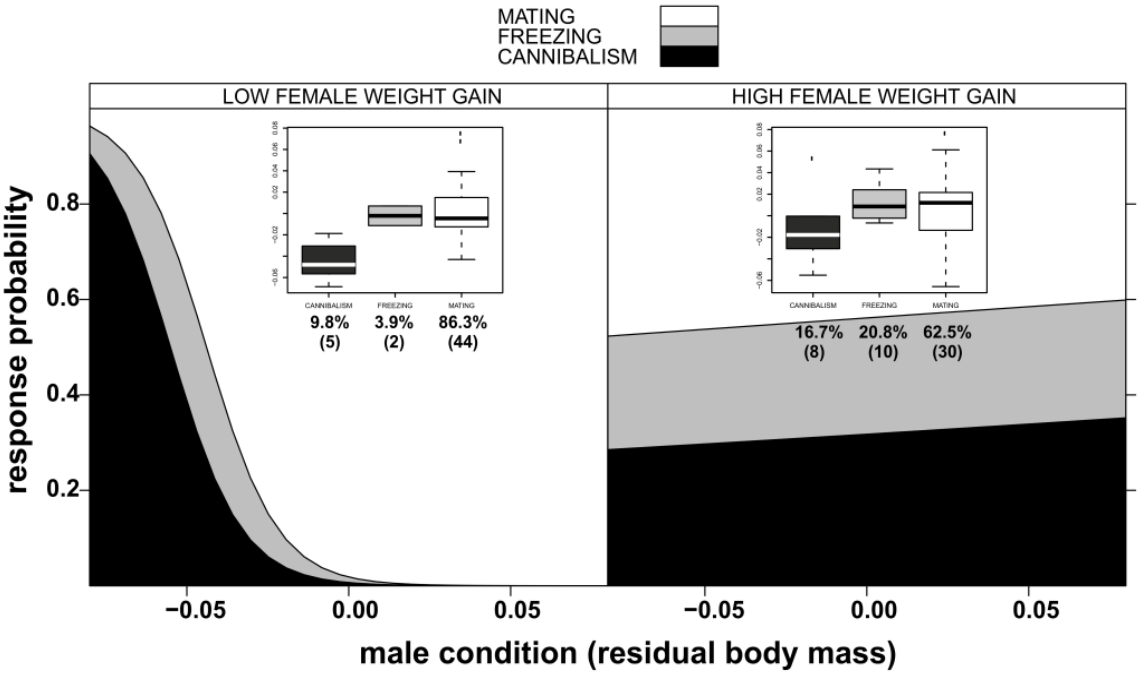

Figure 2. Selection on male condition at two levels of rate of weight gain in females. Effects of a proportional odds generalized linear model plot showing the effect of presumed female voracity (rate of weight gain) on selection on male body condition. The areas depicted correspond to the probability of mating (white), freezing (grey) and cannibalism (black). Note how the probability of cannibalism and freezing increases with the level of female voracity (and how the probability of mating decreases). Apparent in the graph is also the strong selection upon male body condition exerted by the least voracious females, and how this selection decreases with female voracity (compare left and right panel). Effects were depicted for extreme female phenotypes (for the highest and lowest decile) and using the library 'effects' (Fox 2003). The insets show the actual male body condition data. The inset in the left panel corresponds to the data below the median rate of weight gain for females. The inset in the right panel corresponds to the data above the median rate of weight gain for females. Percentage and number of events for each outcome are given below each box in the inset.

Discussion

Our results do tentatively support the hypothesis that female aggressive spillover behaviour affects her ability to impose mate choice upon males through sexual selection.

These results were found despite the fact that the female rate of weight gain was a suboptimal proxy of female voracity in a common garden with unlimited food. The most voracious females tended to kill males while the least voracious (which gained less weight prior to exposure to a male) tended to mate with males. In addition, females imposed selection upon males, as male in better condition had higher mating success and a lower probability of being killed by females. This

supports the idea that females act as selective agents on male condition. Finally, a novel finding, which is an implicit consequence of female spillover behaviour, is that the most voracious females in the population are not actively selecting male phenotypes to kill or to mate with. Rather, these females display a higher rate of attacks upon males regardless of the male phenotype and also tend to mate much less than the least voracious females in the population. Females that gain weight at a low rate, however, impose strong selection on males, killing males in poor condition and mating with males in better condition.

Female voracity could predict the occurrence of premating sexual cannibalism

As predicted, our estimate of adult female voracity; i.e. rates of weight gain prior to the contact with a male, predicted whether a female would attack and kill a courting male. Individual rates of weight gain depend on two traits (voracity and assimilation efficiency) and on environmental variation (prey quantity and quality, exposure to predators and abiotic factors) (see Figure 1).

We assumed that environmental variability among females was likely negligible because of our common garden experimental setup. First, all females relied on the same unlimited supply of natural prey and second, females were isolated in enclosures close to one another in the field. The rate of weight gain could therefore reflect either or both voracity and/or assimilation efficiency. However, in *Lycosa godeffroyi,* an ecologically close relative of *L. hispanica*, assimilation efficiency has been shown to be little variable (within environments CV=2-10%; among environments CV=5%) (Humphreys 1977), and because in our study the rates of weight gain were highly variable (CV = 189%), we assumed that differences in individual growth rates mostly reflected differences in voracity. Furthermore, a combination of assimilation efficiency and environmental variability might also favour variation in the rates of weight gain. For instance, it has been shown that wolf spiders achieve lower rates of weight gain when feeding on prey with low protein content (Mayntz and Toft, 2001); and that spiders, which are highly resistant to starvation, may be capable of lowering their metabolic rate during periods of low prey supply hence improving survival (e.g. Anderson 1974,

Wise 1993, Wang et al. 2006; but see Jensen et al. 2010). Although these patterns would add complexity to the drivers of weight gain, our common garden experiment likely minimised these effects, and hence we can confidently rule them out as important sources of inter-individual variability. On the other hand, voracity may reflect a combination of several traits like boldness, aggression and hunting ability (Figure 1), that may or may not be correlated among each other (e.g., Johnson & Sih 2005). Boldness, which is correlated to foraging activity outside the burrow, explains hunting success (Moya-Laraño 2002), suggesting that at least in part boldness explains the variance in voracity. Aggressiveness has been documented to be positively correlated to boldness in other spiders (Johnson and Sih 2005) and to even have a quantitative genetic basis in some spiders (Riechert and Maynard-Smith 1989; Riechert & Hedrick 1993; Kralj-Fišer & Schneider 2012), and hence voracity could also be explained by hunting ability. However, the extent to which boldness and aggression are correlated, as well as the part of the variance in voracity that may be explained by aggression alone, are currently unknown. Although the heritability of boldness, aggression and voracity remains unknown in *L. hispanica*, indirect evidence of family effects, independent of female (mother) foraging history, on spiderling growth rates (Rabaneda-Bueno et al. 2008; see also Uhl et al. 2004) suggests a genetic basis for at least growth variability. In addition, cannibalistic tendencies (an estimate of aggression) have also been shown to have substantial family effects in a web-building spider (Johnson et al. 2010). Unfortunately, due to the long life cycles (Orta et al 1993; Parellada 1998), more than two years of laboratory rearing would be required to estimate heritability in *L. hispanica*.

Surprisingly, and contrary to what was suggested by previous studies (Moya-Laraño et al. 2003a,c), neither female body size nor condition explained the probability of sexual cannibalism. Further studies manipulating body size and food availability should address this last question. However, the present study illustrates that regardless of size and condition, female personality (voracity used as a surrogate of aggression which was estimated from rates of weight gain) predicts whether females indiscriminately attack males (Arnqvist & Henriksson 1997; Johnson & Sih 2005). Although merely tentative, as the correlation between the rate of weight gain prior to male-female encounters and aggressiveness toward

heterospecific prey need to be documented, the present study suggests the existence of female personality polymorphisms with varying levels of behavioural plasticity, as recently found in *Larinioides sclopetarius* Clerck (Araneidae) (Kralj-Fišer & Schneider 2012).

Sexual cannibalism as a potential form of mate choice on male condition

Males in better condition (residual body mass) were more likely to mate with females and less likely killed. This suggests that females use sexual cannibalism as a mechanism of mate choice (Prenter et al. 2006). Why females would prefer to mate with males in better condition (i.e. and not with those of larger fixed body size) may be explained by the fact that male condition is a highly reliable trait to assess male fitness. A field study shows how in males, residual body mass is highly repeatable across the mating season, suggesting a genetic basis for body condition (Corcobado 2011; but see Naya 2010). Second, males in better condition are faster at escaping from predators and at mate searching and also have higher mating success in the wild (Corcobado 2011), suggesting that by choosing males in good condition, females may accrue indirect genetic benefits. In addition, as with juveniles (Moya-Laraño et al. 2003b), the black ventral markings of the males, which are conspicuous to the female both before and during mating, are strongly correlated with male condition (J. Moya-Laraño and R. Rabaneda-Bueno, unpublished data), suggesting that females can easily assess male condition from body markings. However, despite the fact that body condition is highly repeatable, when males become very old, they stop feeding and their condition suddenly drops in the field. Actually, senescent males can be distinguished in the field because of their very poor condition (Moya-Laraño, personal observations). Thus, in addition of females using body condition to tease apart males of low genetic quality, choice on condition could also serve to discard the oldest males.

Contrary to docile females, voracious females may exert little selection on male phenotypes

We predicted that if voracious females indiscriminately spill over their aggression towards males, then we should find that the presumed most voracious

females in the population (i.e. those with higher rates of weight gain in our common garden) should exert comparatively little selection upon male phenotypes, as they would attack males regardless of their phenotype. The results in Figure 2 strongly suggest that this is the case. Furthermore, males tend to freeze at a higher rate when exposed to voracious females (see the increase of the grey area from left to right in Figure 2), which suggests that males somehow recognise that approaching these females is risky. Whether this is the case in *L. hispanica* and what cues males may be using to assess the potential danger of a female, deserves future research.

Why the larger females in the population are not more aggressive is surprising, especially, if we consider that the spillover hypothesis (Arnqvist & Henriksson 1997) specifically predicts that larger females are more voracious (as voracity leads to faster rates of weight gain). However, faster rates of weight gain can lead to larger adult body sizes and/or earlier maturation. Since in *L. hispanica* fixed body size is not related to fecundity (Moya-Laraño 2002; Rabaneda-Bueno et al. 2008), fast-growing and early maturation may be a better (more profitable) strategy for the more aggressive females (i.e. spillover). Actually, recent simulation work show how early-maturing spillover females can invade populations of females that do not attack males until they have accrued sperm, while large-maturing spillover females cannot (J. Moya-Laraño, R. Rabaneda-Bueno, S.K. Diep, E. Morrison and P.H. Crowley, unpublished data). Clearly, our findings add useful information to the lively current debate on the evidence and prospects for future research concerning the ASH (Kralj-Fišer et al. 2013, Johnson 2013 and Pruitt and Keiser 2013),

Conclusions

This study adds to the growing evidence linking animal personalities, sexual cannibalism and sexual selection (Kralj-Fišer et al. 2012) by presenting and tentatively testing a novel hypothesis, namely that female aggressive personalities, which spill over on aggression towards males, may also reflect variability in the levels of sexual selection upon males, being the most selective females those which

are least aggressive. Since sexual cannibalism is an extreme sexual conflict, in which the costs and the benefits for each sex are radically different (Elgar 1992; Schneider & Lubin 1998; Elgar & Schneider 2004), understanding the evolution of this behaviour may shed new light on the ecology and evolution of animal personalities and how they interact with sexual selection. Finally, our findings may provide a framework to test hypotheses related to behavioural syndromes. For instance, to find answers to questions like Does genetic variation in female personality (the G-matrix), acting as a matrix of selective agents (the O-matrix *sensu* MacColl 2011; see also Moya-Laraño 2012) affect the maintenance of genetic variation (the G-matrix) in male sexually selected traits? This framework could help explain why certain phenotypes are maintained in populations despite strong selective pressures against them.

Acknowledgements

We thank P. Crowley and M. Foellmer for helpful comments on a previous draft of the ms. Several anonymous referees, including 8 peers at Peerage of Science reviewed previous versions of this ms. We thank Raúl Rabaneda, Manuel Méndez, Alfredo Durán and Alejandro Moreno for logistic support in the field, and Isabel Cueva and Matthias Boer for kindly allowing us to use their land for the experiments. This research was financially supported by the Spanish Ministry of Science and Education grant (MEC)/FEDER CGL2004-03153, a Ramón y Cajal research contract to JML and a pre-doctoral fellowship I3P-BPD2004-CSIC to RRB.

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MANUSCRITO III

Polyandry affects offspring variability in a sexually-cannibalistic species

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Resumen

La poliandria puede ser una estrategia de "bet-heging" mediante la cual las hembras que se aparean con varios machos incrementan la diversidad genética de su descendencia, y con ello las probabilidades de que al menos una proporción de ésta sobreviva hasta la madurez en ambientes heterogéneos e impredecibles. Por otro lado, si la poliandria es beneficiosa, el canibalismo sexual podría entrañar un coste adicional antes ignorado al disminuir las posibilidades de las hembras de aparearse con varios machos, ya que contribuir a disminuir el acceso a los machos. Usando los datos de tres experimentos de campo y un experimento de laboratorio en la araña caníbal sexual *Lycosa hispanica*, se comprobó si las hembras poliándricas producen descendencia de calidad más variable, y si la media geométrica de su eficacia biológica entre dos ambientes de distinta disponibilidad de alimento para la descendencia es superior a la de las hembras monándricas. Los resultados de un experimento de campo, en el que se manipularon las densidades de machos, y de un experimento de laboratorio, en el que las arañitas disponían de más o menos alimento, muestran que el grado de poliandria de la hembra explica positivamente la variabilidad tanto en el tamaño de la descendencia como en sus tasas de crecimiento. Sin embargo, en un segundo experimento de campo, donde se manipuló directamente la poliandria, no se encontró una asociación entre poliandria y variabilidad de la progenie, probablemente porque la disponibilidad per cápita de genotipos de los machos fue mucho más baja. Finalmente no encontramos evidencia de que la poliandria afectara positivamente la eficacia biológica media de las crías pertenecientes a la misma puesta entre ambos tratamientos de alimentación. No obstante, puesto que la poliandria estuvo vinculada a la variabilidad de la progenie en al menos uno de los estudios, el apareamiento con machos diferentes podría ser beneficioso para las hembras en condiciones naturales. Posiblemente las condiciones de laboratorio del presente estudio no lograsen capturar la variabilidad existente en ambientes naturales. Por tanto, la pérdida de oportunidades para aparearse con machos diferentes supondría un coste no explorado atribuible al canibalismo sexual.

Palabras clave: *poliandria, bet-hedging, canibalismo sexual, eficacia biológica, variación genética, Lycosa hispanica*

Abstract

Polyandry may be a bed-hedging strategy by which females enhance the genetic diversity of their offspring, thereby increasing the chances that at least some offspring survive to maturation in unpredictable heterogeneous environments. On the other hand, since sexual cannibalism may contribute to decrease access to males, it could entail a previously overlooked cost in the form of decreasing the chances to females of mating multiply if polyandry is advantageous. Using data from three field and one laboratory experiments on the sexually-cannibalistic spider *Lycosa hispanica*, we tested whether polyandrous females have offspring that are more variable in quality and whether the geometric mean fitness of polyandrous females across two environments which differed in food availability for the offspring was high relative to monandrous females. In a field experiment in which we manipulated male densities, combined with a laboratory experiment in which we reared the spiderlings under high *vs*. low food regimes, we found that the degree of female polyandry positively explained the variability in both offspring size and offspring growth rates. However, in a second experiment in which we directly manipulated polyandry, we failed to find an association between female multiple mating and offspring variability, likely because the *per capita* availability of male phenotypes was much lower. Finally, we found no evidence that polyandry positively affected the geometric mean fitness of siblings across environments. Since polyandry was linked to offspring variability in at least one study, multiple mating could still be advantageous for females in the natural range of environments. We may have just failed to mimic such environments in laboratory conditions. Thus, an additional cost from sexual cannibalism could be the loss of opportunities to mate multiply.

Keywords: *polyandry, bet-hedging, sexual cannibalism, fitness, genetic variation, Lycosa hispanica*

Introduction

Polyandry, or female mating with multiple males, is a common phenomenon in nature whose benefits may be diverse (Arnqvist & Nilson 2000; Hosken & Stockley 2003; Simmons 2001). Despite these potential advantages, mating with multiple males may have elevated costs for females too (Rowe 1994; Arnqvist 1997; Chapman et al 1995; Jennions & Petrie 2000; Hosken & Tregenza 2006), and in cases in which a single mating might be sufficient for egg fertilization, polyandry is not well understood (Halliday & Arnold 1987; Jennions & Petrie 2000; Zeh & Zeh 1996), especially when males do not provide extra-benefits beyond those of transferring sperm (Arnqvist & Nilsson 2000; Simmons 2005).

Beyond securing full egg fertilization (Hasson & Stone 2009), the benefits of polyandry can be divided in two main groups: nutritional or material (direct) benefits and genetic (indirect) benefits (reviewed in Arnqvist & Nilsson 2000; Fedorka & Mousseau 2002; Hosken & Stockley 2003; Moya-Laraño & Fox 2006). The genetic contributions of polyandry to the female fitness are still unclear (e.g. Brown et al 2004; Maklakov & Lubin 2004), as except for a few studies that have successfully disentangled between material and genetic benefits (e.g. Newcomer et al. 1999; Bradley & Parker 2001; Moya-Laraño & Fox 2006), material benefits can often mask genetic driven effects, which might be obvious only in subsequent generations (Hosken & Blanckenhorn 1999; Jennions & Petrie 2000; Zeh & Zeh 2001; see also Barbosa et al 2012).

Genetic benefits can be directly related to male quality, and could provide increased genetic diversity or mean fitness of progenies (i.e. genetic bet-hedging, Watson 1991, 1998), lower probability of inbreeding (Stockley et al 1993; Tregenza & Wedell 2002; Cornell & Tregenza 2007; Bilde et al 2007), and higher likelihood of mating with good quality mates; especially if mate choice on additional males is at play, or siring offspring from genetically compatible males (Zeh & Zeh 1996, 1997, 2001; Tregenza & Wedell 2000; Moya-Laraño & Fox 2006). Among these variety of genetic benefits, the bet-hedging hypothesis states that, by favoring offspring genetic diversity, polyandry could serve to increase the chances that at least some offspring survive to reproduction in heterogeneous,

unpredictable environments (Seger & Brockmann 1987; Philipi & Seger 1989; Watson 1991; Olofsson et al 2009; see also Schneider & Elgar 1998). Few studies, however, have truly examined whether polyandry may provide genetically diverse offspring, and more extensive work is needed to understand the evolution and maintenance of polyandry. Most available evidence comes from model simulations whose results are often unmatched with nature and difficult to interpret (e.g. Olofsson et al 2009; Rees et al 2010), and therefore testing the bet-hedging hypothesis of polyandry may actually require further empirical work. The theory of bet-hedging is based on the fact that natural environments are often variable and unpredictable from year to year (Roff 1992). In a risk-averse or diversifying bet-hedging strategy, the geometric mean fitness would be expected to increase over generations as a result of its variance being reduced between bad and good years, dimming to some extent the effects of environmental variability. Hence, females may allocate resources in multiple directions to increase the progeny phenotypic variance, which could prevent the death of all offspring if an eventual stochastic change occurs, favoring survivorship of at least some progeny (i.e. diversified bet-hedging) (Koops et al 2003; reviewed in Fox & Czesak 2000).

Alternatively, multiple mating associated to genetic diversity can be a non bet-hedging strategy when within-brood variability in size traits may contribute to relax sibling competition (Ridley 1993; Yasui 1998; Forsman et al 2007), which would then favor niche partitioning with regards to the use of resources, thereby reducing competition and enhancing the productivity (i.e. survival) of a progeny (Hughes et al 2008; McLeod & Marshall 2009).

From an evolutionary perspective, selection should favor the evolution of strategies that reduce the variance in fitness across generations and select against those in which the low fitness in a single generation tend to generate elevated costs in the long-term. Whether polyandry is such a type of strategy to increase mean geometric fitness of offspring when exposed to variable environments is little explored. To detect the effects of polyandry on fitness may be problematic, since bet-hedging benefits may depend on particular or infrequent environmental conditions difficult to recreate (McGinley et al. 1987; Holman & Kokko 2013).

Sexual cannibalism, females killing males before during or after mating (Elgar, 1992; Elgar & Schneider 2004), is a behavior that may reduce male availability to both the actual female that kills the male if she does it before she has accrued sperm (Arnqvist & Henriksson 1997) and to every female in the population (Polis 1981). In sexually-cannibalistic species, if polyandry entails benefits to the females, in addition to the obvious risk incurred of a complete lack of fertilization by killing males (Arnqvist & Henriksson 1997), females could also reduce their potential benefits from mating with multiple males, a cost that has been largely neglected in the literature. Therefore, it seems that the benefits of polyandry should be investigated further in species that kill the male before mating (pre-mating sexual cannibalism),

Here, we used published data (Rabaneda-Bueno et al. 2008; 2014) and a laboratory experiment to investigate whether the Iberian tarantula (*Lycosa hispanica,* formerly *L. tarantula*), a premating sexually-cannibalistic burrowing wolf spider, shows patterns consistent with polyandry being a form of diversifying bet-hedging. We first checked whether polyandry could be a mechanism to accrue indirect genetic benefits via mate choice (Zeh & Zeh 1996, 1997, 2001; Tregenza & Wedell 2000; Moya-Laraño & Fox 2006), by testing if polyandry affected mean offspring size or performance (growth rates and survival) within a single generation. Given that at least some *L. hispanica* females are choosy (Rabaneda-Bueno et al. 2014), females could mate multiply to choose among the (genetically) best males, and this could result in an improvement in the traits of offspring mothered by polyandrous females. Second, we tested the simple prediction of the diversifying bet-hedging hypothesis that polyandrous females should mother offspring that are phenotypically more variable. Finally, we conducted a laboratory experiment in which the offspring of females of known mating history in a field experiment were reared under two feeding regimes in a split-brood design. This served to test the bet-hedging prediction that polyandrous females have higher geometric mean fitness across generations, here mimicked by manipulating the concurrent environments.

Material and Methods

Species and study site

The Iberian tarantula *Lycosa hispanica* (formerly *L. tarantula*- Planas et al 2013) is a sexually cannibalistic burrowing wolf spider with a relatively short reproductive period (Fernandez-Montraveta & Ortega 1990; Orta et al 1993, Moya-Laraño 1999; Moya-Laraño 2002; Moya-Lararño et al. 2002, 2003a,b; Rabaneda-Bueno et al 2008). In our study area (southeast Spain) the mating season starts around late May when juvenile spiders, after a period of 21-22 months of development, reach maturation and occupy burrows on the ground. Sexual cannibalism in this species is mainly pre-mating, with a relatively lower incidence among virgin than among mated females (Moya-Laraño et al. 2002; 2003a; Rabaneda et al. 2008).

Overview of the experiments and data used

Reproductive data of a natural population of *L. hispanica* were obtained from field and laboratory experiments conducted during 2005 and 2006. The main data on all of these experiments but one (2005 laboratory experiment) have been already published and many of the details in the experimental procedures can be found elsewhere (Rabaneda-Bueno et al. 2008; 2014). The first experiment (Exp. 1, May-September 2005; Rabaneda-Bueno et al. 2008) was conducted in the field, in which we were able to induce differences in polyandry through manipulating male densities in each of 9 12x12m plots each containing 8 females in artificial burrows. Three plots were assigned to high male density (0.22 m^{-2}), three to medium male density (0.11 m^{-2}) and three to low male density (0.06 m^{-2}). A total of 32, 16 and 8 males were released respectively within each plot containing 8 females. Within a plot, males were allowed to wander around from female to female burrow, and male-female interactions, including sexual cannibalism, occurred similarly as in the wild. Frequent visits to the female burrows allowed documenting most of the matings. Females in each of the treatments mated respectively with 2.4 ± 0.28, 1.3 ± 0.21 and 1.1 ± 0.28 males (Rabaneda-Bueno et al. 2008). A system of two parallel

lines of alive-catching trench traps surrounding each plot allowed monitoring and keeping the flux of natural prey while controlling male densities. Since the details of this experiment and the results on mating patterns can be found somewhere else (Rabaneda-Bueno et al. 2008) we do not repeat them here. From the above experiment, part of the offspring mothered by the 29 females from which an egg sac hatched successfully were brought to the laboratory and half of the offspring of each female split in two treatment levels, high and low food (Exp. 2, October 2005-March 2006). The body size (carapace width) of these offspring at birth, and the change in carapace width (growth) and survival in the laboratory were regressed against the female level of polyandry, as previously observed in the field experiment (range 0-3 matings).

The third experiment (Exp. 3; May-September 2006) was conducted in the same study area but differently than the precedent experiment, females were individually confined in 1x1m field enclosures (Rabaneda-Bueno et al. 2008; 2014) and randomly assigned to two treatments: polyandry ("polyandry", "monandry") and cannibalism ("male provided as food", "male not provided"). Females in the polyandry treatment level received 4 extra-males after the female first mated, whereas for females in the monandry treatment males were only offered until the female first mated. Although females in the "polyandry" level had the chance to mate more than once, not all of them did actually mate more than once. For statistical analysis, we therefore distinguished between obligate monandrous and voluntarily monandrous females. The cannibalistic treatment has been explained in detail somewhere else (Rabaneda-Bueno et al. 2008) and was devised to test the value of feeding on a male on female reproductive success. In brief, this treatment consisted in offering an anaesthetised male to all females and once the male was killed by the female only half the females were allowed to feed on it (those in the "male provided as food" treatment). Females were isolated until offspring hatching, and for each female 20 offspring were preserved frozen for later measurements under the dissection microscope.

Finally, a sample of spiderlings born from the 47 females that successfully hatched an egg sac in the above experiment were released in 1x1m field enclosures at two densities, 21 and 42 m^{-2}, reflecting a low and a high competitive

environments (Exp. 4, september-december 2006 Rabaneda-Bueno et al 2008). The carapace width of spiderlings was measured at the moment of release and again at the end of the experiment. Survival (as number of spiderlings remaining at the end of the experiment) was also monitored.

Laboratory offspring development at two feeding regimes (Experiment 2)

Upon egg hatching, subsets of each mother's offspring from Experiment 1 were frozen and either immediately measured under a dissection microscope (n=10) or kept frozen to be measured later (number varied). Another 20 spiderlings were weighed and isolated in see-through plastic containers provided with sand at their bottom. Wet cotton ensured water supply. In the laboratory, half of these 20 spiderlings isolated from each female were randomly assigned to one of two feeding regimes (split-brood design), LOW *vs*. HIGH food. Spiders in the HIGH feeding treatment received twice as much food (*Drosophila melanogaster* reared on a protein-enriched diet, supplemented with *Tenebrio* sp. and *Calliphora* sp. larvae as the spiders grew older) as spiders in the LOW feeding treatment. The amount of prey supplied in each of the feeding treatments increased proportionately during the study period at a monthly rate, doubling the amount of food, shifting from initial 1 *vs* 2 prey items (LOW vs HIGH), and subsequently increasing the amount to 2 *vs* 4, 3 *vs* 6 to finally reach 5 *vs* 10 prey items at the fourth month of spiderling development, when food quantity had incremented by 5X, and the net supply would then keep constant till the end of the experiment. With these feeding treatments we intended to simulate heterogeneity in the environment experienced by the offspring of each female, mimicking inter-annual variation in food availability, which served to test the prediction of the diversifying bet-hedging hypothesis that polyandrous females increase the geometric mean fitness across environments. Thus, by setting two environments in a single generation, we mimicked two virtual seasons affecting the offspring of each single female, which allowed us to test the prediction of the bet-hedging hypothesis. If female polyandry is a strategy to increase the genetic diversity of her progeny and spread their chances of success, spiderlings from polyandrous females should have higher geometric mean fitness between environments than the spiderlings of monandrous females.

Moulting was controlled on a daily schedule. We noted the date of spiderling moulting and the date of spiderling death. The experiment started on November and continued for several months. However, we here analyse only the data until the end of March. At the end of the experiment, we measured (1) spiderling survival (YES=1, NO= 0), (2) spiderling moulting rate (number of moulting episodes since birth) and (3) spiderling final mass and size, to calculate the growth rate during development between hatching and the fourth month of development, defined as the daily change in carapace width.

Experiment 3: Induced polyandry in field enclosures

The main results, other than the effects of polyandry, have been published elsewhere (Rabaneda-Bueno et al. 2008; 2014). In this experiment adult females (n=80) were randomly assigned one of two polyandry treatments ("Polyandry", "Monandry"), and induced mating by presenting them one or more males sequentially. As explained above, this treatment was crossed with a cannibalism treatment in which males were provided as food to half of the females. We considered this treatment as an additional factor for the statistical analyses performed here (i.e., as a covariate). However, since this factor was never relevant, we refer to the original publication for further details on this treatment (Rabaneda-Bueno et al. 2008). Before the maturation moult, subadult females were housed in artificial burrows (Moya-Laraño et al. 2002) inside individual metal enclosures (1x1x0.3 m) containing natural prey provided *ad libitum*. As soon as females reached maturity they were measured and weighed, and mating trials started approximately one month later. A day before the trial females were measured and weighed again. Males were captured as adults (unknown previous mating history) and located at room temperature in plastic 18x18x30cm PVC containers, filled with up to 2 cm and no burrow. These terraria were humidified daily by spraying water until a male was used in a mating trial. Each male was used only once. Mating was induced in 20x20x5cm wire cages (mesh size 1cm) centred on the female burrow and within which the male was released. We conducted 8 mating trials per day during daylight (from 8.30am to 3pm). The release of a male within the female enclosures did not always result in mating, and females could kill their potential mate (Rabaneda-Bueno et al. 2008; 2014), in which case we

presented her a new male the next day until we granted a complete mating. After mating, females within the "Monandry" treatment did not receive any more male. In the "Polyandry" treatment females were presented 4 additional males each every 5-days. Females could kill or mate with these males, but sometimes neither of these happened because the male remained frozen at the female burrow's mouth (Rabaneda-Bueno et al. 2014). Therefore, all females mated at least once, but only females in the polyandry treatment had opportunities for re-mating with different males. Females within the "monandry" treatment that had concluded their respective mating trials (after first mating) received visits at a similar rate as females in the "polyandry" treatment, thus all being equally disturbed in case the observer could be assessed as a threat by the spider.

Spiderling growth and survival in controlled field enclosures (Experiment 4)

After eclosion of egg sacs, a subsample (numbers vary) of spiderlings from each mother (experiment 3) were frozen and either immediately measured (n=10, carapace and width to the nearest 0.01mm) or kept frozen for later measures. Eventually, up to 20 spiderlings per female were measured. To study the effects of polyandry and experimental cannibalism on recently hatched spiderlings (Rabaneda-Bueno et al. 2008), siblings of each mother from both the "monandry" and the "polyandry" treatments were released into the 1x1m enclosures formerly housing the female burrow at one of two density levels (High=42m^{-2} or Low=21m^{-2}), and allowed to grow until early December. The experimental results related to the effects of cannibalism have been published somewhere else (Rabaneda-Bueno et al. 2008). Therefore, here we focus on the effects of polyandry.

Estimates of spiderling body size and growth

As different experiments used different approaches to estimate size (e.g., body mass could only be reliably estimated in the laboratory experiment), we used the one estimate that was homogeneous to all studies: carapace width. Similarly, growth was assessed as the change in carapace width through time. In all data bases, carapace width was measured to the nearest 0.01mm under a dissection microscope. In Experiment 1 RRB measured the carapace width of a random sub-

sample of recently frozen hatchlings (n=10 per female) and, when available, an additional 10 frozen spiderlings per female were measured by a laboratory technician at EEZA. On average, 18.2±0.5 spiderlings were measured for each female. The exact same procedure was undertaken for Experiment 3 (average number of spiderlings per female 18.5±0.5). These measures were taken under a Zeiss Stemi DV4 dissection microscope. In order to estimate repeatability between measurers we took the family means (across both studies) as estimated by each measurer, each of whom used a different set of individuals. Given that repeatability was not too high (0.61 ± 0.1, P<0.0001; calculated with library "rptR" in R), and that this was likely due to both measurer error and error on the estimate of the mean from such a small sample size (N=10 at most), we decided to include measurer as a candidate covariate in all the statistical models concerning the above data. Growth in the 2005 laboratory experiment (Experiment 2) was estimated by measuring spiderling carapace width after each molt by immobilizing each individual in a plastic bag using an Olympus SZX9 dissection microscope provided with a micrometer. In the latter experiment all measures were taken by RRB whose intra-observer repeatability is substantial (0.93±0.02, p<0.0001). For the 2006 field enclosure experiment (Experiment 4) the final body sizes were estimated by measuring the spiderlings alive by placing one at a time in a Petri dish and the dish under the dissection microscope (Zeiss Stemi DV4). In this last experiment, all measurements were taken by JML, whose repeatability measuring spiders has been tested to be above 0.95 (e.g. Moya-Laraño et al. 2008).

Growth rate (GR) for each individual was estimated as $GR_i=(C_{fi}-C_{oj})*days^{-1}$, where C_{fi} is the final carapace width (in mm) for individual *i* and C_{oj} is the initial carapace width for the family *j*, to which individual *i* belongs. C_{oj} was estimated for Experiment 2 and Experiment 4 from the 20 offspring per family measured in Experiments 1 and 3 respectively.

Statistical analyses

In order to test for *the mate choice hypothesis of polyandry (indirect effects)*, we built a series of models to test for fitness-enhancing effects of polyandry on offspring. For the 2005 data set we analysed whether polyandry affected average

spiderling body size at birth by including spiderling carapace width in Generalized Linear Mixed Models (GLMMs) with Normal errors and identity link functions (libraries "lme4" and "lmerTest" in R - R development core team 2014). As fixed explanatory variables in the model we included the male density treatment (ordered categorical variable), the polyandry status of the mother (i.e., the number of males which she was observed to mate with) and the identity of the spider measurer. Field plot and female identity were included as random factors. We checked for alternative models via Akaike's Information Criterion (AIC, Burnham & Anderson 2002). For growth rates the approach was similar with the exception that laboratory feeding treatment was also included in the analysis. Survival patterns were analyzed as "time to death" via Cox Proportional Hazards regression mixed models (library "coxme" in R), including the date of death and a censoring variable indicating whether death had occurred or not by the end of the observation period (Allison 1995). Field plot and female identity were included as random factors.

For the 2006 field data set on body size we also tested among alternative GLMM models by means of AIC, in which the independent fixed factors were the cannibalistic treatment, the polyandry treatment and measurer. Since some females within the polyandry treatment mated while others did not, we distinguished between experimentally monandrous females (i.e., those females that had never the chance to mate more than once because no additional males had been offered) and voluntarily monandrous (i.e., those females that given the chance did not mate more than once). Our polyandry treatment had therefore three levels: experimentally monandrous, voluntarily monandrous and polyandrous. Female identity was included as a random factor. Growth rates were analysed in GLMMs within which we combined as fixed factors the cannibalistic and polyandry treatments, as well as the interaction between them. Female identity was also included here as a random factor and AIC used again to choose among models. Survival was analysed with a binomial GLMM in which the dependent variable was the number of alive and dead spiderlings within each 1x1m field enclosure. Again we searched for the model with lowest AIC including a combination of the polyandry and cannibalistic treatments as well as spiderling

density (21 *vs* 41 m^{-2}). As replicates were established at different dates, i.e. as spiderlings hatched, but the final census was established in the same date, "days since release" into the enclosures was forced as a covariate in all models to control for daily mortality.

The *diversifying bet-hedging hypothesis of polyandry* was tested in two steps. First, we tested whether polyandrous females had more variable offspring. Second, we tested whether polyandrous females had higher geometric mean fitness across feeding environments (2005 laboratory experiment), as expected if accruing higher offspring variability from polyandry would be a form of bed-hedging. For the 2005 data set, we analysed whether polyandry affected variability in spiderling body size at birth by including in GLMMs with Normal errors the standard deviation of spiderling carapace width as calculated for the 20 offspring of each female. As fixed explanatory variables in the model we included the male density treatment (ordered categorical variable), the polyandry status of the mother (i.e., the number of males which she was observed to mate with), the identity of the spider measurer and the mean spiderling carapace width for each female. Field plot was included as a random factor. We checked for alternative models via AIC. For growth rates the approach was similar with the exception that laboratory feeding treatment was also included in the analysis of standard deviation in growth rates. To test for an effect of polyandry on geometric mean fitness in the laboratory experiment we calculated geometric mean fitness across high and low feeding environments for each female. The variables used for fitness were offspring growth rate, offspring mortality and the product of growth rate and offspring survival.

For the 2006 data set we tested among alternative GLM models by means of AIC, in which the independent fixed factors were the cannibalistic treatment, the polyandry treatment, measurer and offspring average carapace width. The dependent variable was the standard deviation in carapace width calculated among the 20 offspring of each female. We also chose among GLM models for growth rates in which average growth rate across the offspring of each female was also included as a potential covariate along with the cannibalistic and polyandry treatments.

Results

The mate choice hypothesis of polyandry - indirect effects

We found no evidence for the mate choice hypothesis of polyandry. None of the polyandry variables entered any of the models and therefore had no explanatory power on offspring traits or survival. For the 2005 field data set on spiderling body size, the model with the lowest AIC included only measurer as a fixed factor (Electronic Appendix Table A1). In the final model, female identity (χ^2_1=109; P<0.0001) but not plot, was a highly significant source of variation, explaining 27.5% of the random variance in offspring body size. The results for the 2006 field data set were qualitatively identical, with the best model being the null model, followed by that including only measurer as fixed factor (Electronic Appendix Table A2) and female identity explaining 27.1% of the random variance in offspring body size (χ^2_1=176; P<0.0001).

Regarding growth rates, the analysis of the laboratory experiment on the 2005 data set showed that the best model only included feeding regime as a fixed factor affecting the growth rate of the spiderlings (Electronic Appendix Table A3). Female identity explained 53% of the random variance in spiderling growth rates (χ^2_1=285.3; P<0.0001). For the 2006 field experiment (release of spiderlings in 1x1m enclosures), the best model was the null model (Electronic Appendix Table A4), including only the random factor female identity, which explained 43.8% of the variance in growth rates (χ^2_1=12.7; P<0.0001).

For mortality, in the laboratory 2005 experiment the best model (Electronic Appendix Table A5) for time to death (Cox Proportional Hazards regression) was that which included the intercept only (i.e., no fixed effects). There was a significant effect of the random factor female identity on the hazard rate (χ^2_1=88.8; P<0.0001), indicating that the timing of death was not random according to relatedness. In the 2006 field enclosures, the best model (Electronic Appendix Table A6) included, in addition to the forced term "time since release", the term "density", which had a tendency to negatively explain survival (estimate = -0.02; Z=-1.85; P = 0.064). Since the offspring of a single female was released within the

same enclosure (i.e., a sampling unit was both a female and an enclosure), we could not estimate the effect of female identity as a random factor on mortality.

The diversifying bet-hedging hypothesis of polyandry

We found partial support for the diversifying bet-hedging hypothesis of polyandry as polyandry was associated with offspring variability in size in one of the experiments. In the 2005 field data, we found that polyandry was the only predictor entering the best model for explaining variability in offspring body size (Electronic Appendix Table A7) and that the effect was positive and significant (estimate = 0.009; χ^2_1=4.36; P=0.037, Fig. 1). The 2006 experiment, however, failed to support the bed-hedging hypothesis, as polyandry did not enter any of the best models for variability in offspring size (Electronic Appendix Table A8) nor was significant in any of them (all Ps > 0.13).

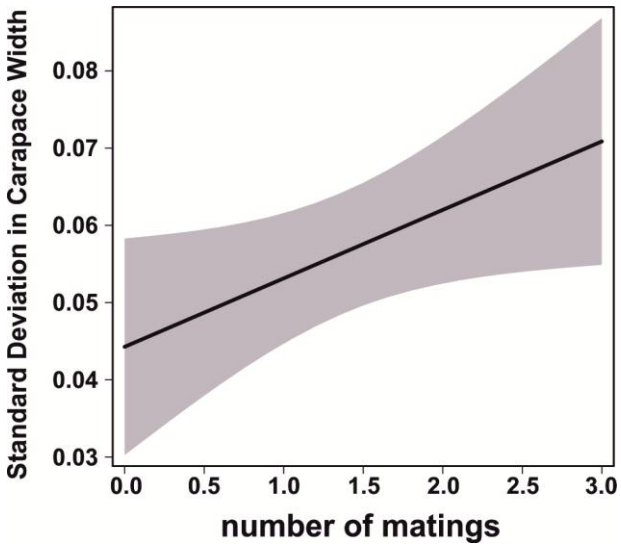

Figure 1. Relationship between polyandry and variability in spiderling carapace width. Zero matings reflect 3 females that were never observed mating but that they laid a fertile egg sac nonetheless, demonstrating that we had missed some matings in our field survey.

For growth rates in the laboratory experiment (Experiment 2), the null model (which included only random effects) was the best model (Electronic Appendix Table A9). Polyandry was the only term in the second best model and again the effect was positive and significant (estimate = 0.0004; χ^2_1=7.48; P=0.006, Fig. 2). The third best model included "feeding treatment" in addition to polyandry, a term that was highly significant (χ^2_1=15.9; P<0.0001) and which was explained

because spiderlings under the low feeding treatment had lower variability in growth rates (Carapace Width SD, mean ± SE: 0.0017 ± 0.0001) relative to the spiderlings grown in an environment with high food availability (0.0022 ± 0.0001). In this last model, the random factor "female identity" was significant (χ^2_1=8.3; P=0.004) and explained 55.2% of the random variance. Again, for growth rates the 2006 data set (field enclosure experiment) failed to support the hypothesis of diversifying bet-hedging, as polyandry did not enter any of the best models (Electronic Appendix Table A10) nor was significant in any of them (all P > 0.21).

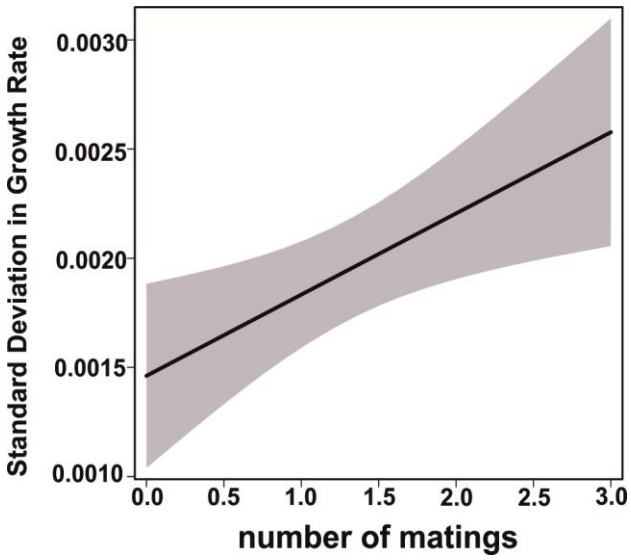

Figure 2. Relationship between polyandry and variability in spiderling growth rates. Zero matings reflect 3 females that were never observed mating but that they laid a fertile egg sac nonetheless, demonstrating that we had missed some matings in our field survey.

When correlating the degree of female polyandry to the geometric mean fitness across high and low feeding environments (laboratory feeding experiment), we found no support for the diversifying bet-hedging hypothesis. Neither growth rate geometric mean fitness (estimate = 0.0005; χ^2_1=0.45; P=0.502) nor mortality geometric mean fitness (estimate = 0.009; χ^2_1=0.02; P=0.876) were significant. The geometric mean on the composed fitness estimate (survival*growth) was not significant either (estimate = 0.0005; χ^2_1=0.37; P=0.543).

Discussion

The results from three field and one laboratory experiments in *L. hispanica* showed that variability in both offspring size at birth and offspring growth rates were linked to female polyandry in one of the studies, consistent with previous findings in another spider (Watson 1998) and with the bet-hedging hypothesis. In another set of experiments in which we partially controlled the number of matings that each female could achieve, however, we failed to find any relationship between polyandry and offspring variability. Furthermore, in none of the studies did female polyandry affect within-generation survival, nor average offspring size and growth rates, which is inconsistent with the mate choice hypothesis of polyandry by virtue of indirect (genetic) effects (Zeh & Zeh 1996, 1997; Zeh et al 1998; Moya-Laraño & Fox 2006). Finally, in the laboratory experiment (Experiment 2) we failed to find any effect of polyandry on offspring fitness (growth and survival) across environments, as the geometric mean across food treatments did not differ between once- and multiple-mated females for any of the variables measured: growth rates, survival and the composite fitness estimate growth*survival. Therefore, although the finding that offspring phenotypic variability is linked to polyandry supports the bet-hedging hypothesis, the experiment tracking fitness across environments failed to support the bet-hedging hypothesis.

An additional finding was that female identity explained relative large amounts of the random variance in offspring body size at birth (27-28%) and in growth rates (44-53%). This finding may reflect maternal and/or genetic effects (heritability) in these traits, which cannot be successfully distinguished without further research, such as conducting additional experiments with specific breeding designs (see also Rabaneda-Bueno et al. 2008).

Why we did find effects of polyandry on fitness variability in Experiment 1 and 2 but failed to find such effect in Experiment 3 and 4 is puzzling. However, there are a couple of possible explanations. First, in Experiment 1, 8 to 32 males were released in 12x12m plots and in principle all females had unrestricted access to each of them. In Experiment 3, on the other hand, 4 additional males were

offered to the females in the polyandry treatment and each female had only a single opportunity to mate with each male. Therefore, the potential to mate with males of divergent genotype was much higher in the former experiment, particularly if some sort of mate choice was at play (Rabaneda-Bueno et al. 2014). In addition, in Experiment 2 the offspring of Experiment 1 were raised in isolation, whereas in Experiment 4 the offspring of Experiment 3 were kept within "family" enclosures, giving the chance for spiderling-spiderling interactions including cannibalism. Therefore, in this last experiment, variability in genetically-determined growth rates could have been masked by high rates of cannibalism, suggested by the higher mortality rates in Experiment 4 as compared to Experiment 2 (94% of the spiderlings died in 3 months in Experiment 4 and only 23% of the spiderlings died in 5 months in Experiment 2).

Furthermore, the lack of finding that the geometric mean fitness of polyandrous females increased across the two feeding environments, as predicted by the bet-hedging mechanism, may mean that bet-hedging does not occur in this species. If that were the case, the association between polyandry and variability in size at birth and growth rates could be a non bet-hedging genetic diversity mechanism (Yesui 1998), which could also be adaptive if for instance reduces sibling competition and promotes individual specialization (Ridley 1993; Forsman et al 2007; Hughes et al 2008). However, in a highly cannibalistic species such as *L. hispanica* (Moya-Laraño et al. 2002), in which spiderlings also readily engage in cannibalism, and considering that differences in body size and growth rates among spiderlings translate into higher rates of cannibalism (Rabaneda-Bueno et al. 2008), variability should promote cannibalism among offspring, which could decrease rather than increase the fitness of polyandrous females. Even though we failed to find that polyandry affected survival in the offspring of our field enclosures, in this experiment we also failed to find that polyandry promoted body size variability among offspring. Therefore, we cannot rule out the possibility that given the chance, the variable offspring of polyandrous females in Experiment 1 would have killed each other at a higher rate that the offspring of monandrous females. We therefore suggest that the lack of finding support for the prediction of higher geometric mean fitness in polyandrous females may be due to either a

failure to recreate the right environmental variability found in nature or that we failed at measuring the right fitness estimates, such as survival to maturity and offspring reproductive success across several generations. Indeed, using a stronger design in seed beetles (geometric mean fitness assessed across three generations with a much larger sample size), Fox & Rauter (2003) found only a slight increase in the geometric mean fitness of polyandrous relative to monandrous females (1.3 - 4.1%), which the authors believed to be sufficiently relevant in magnitude to imply bet-hedging benefits. Such a small effect would remain undetected in our experiment with relatively lower sample sizes. Furthermore, recreating a more realistic environmental variability for *L. hispanica* would not only entail manipulating food availability, but also predator and disease selective pressures. Alternatively, polyandry linked to size and growth variability could actually reflect differences in dispersal propensity, which has been shown to be bimodal in both *L. hispanica* (Parellada 1998; Moya-Laraño & Cabeza 2003) and the sister species *L. tarantula* (Humphreys 1983), with some siblings dispersing before winter and others remaining with the female in the burrow until spring (Humphreys 1983; Parellada 1998). Humphreys proposed that this biphasic dispersal could be a game of the Russian roulette, in which by splitting dispersal in two different seasons, females could increase her fitness against the stochasticity of Mediterranean environments (see also Moya-Laraño & Cabeza 2003). This is nothing but a form of bet-hedging and if by multiple mating females are better able to have a diversity of dispersing offspring, polyandry could evolve by this bet-hedging dispersal mechanism.

Even though our study is partially correlational (e.g. we could not force voluntarily monandrous females to copulate more than once) we found partial evidence for the diversifying bet hedging hypothesis by documenting that polyandrous females have offspring with higher variability in size and growth rates. However, this was only obvious in one of the studies. The lack of support to the prediction that polyandrous females should have higher geometric mean fitness across environments can be explained by our lack of mimicking the environmental variation as occurring in nature. If future research in *L. hispanica* provides further support for the benefits of polyandry via bet-hedging, the loss for the opportunity of multiple mating should be added to the list of costs accrued

from sexual cannibalism. Therefore, not only the lack of fertilization should matter when males are scarce.

Acknowledgements

We thank Virginia Pérez and Nereida Melguizo for helping in the field and in the laboratory. We also thank Isabel Cueva and Matthias Boer for all their help over the years for the prolonged use of their land for our experiments, and Alfredo Durán for his continued support in the field. This research was financially supported by the Spanish Ministry of Science and Education grant (MEC)/FEDER CGL2004-03153, a Ramón y Cajal research contract to JML and a pre-doctoral fellowship I3P-BPD2004-CSIC to RRB.

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ELECTRONIC APPENDIX

Table A1. Generalized Linear Mixed Models for the 2005 dataset analyzing the effects of polyandry (fixed explanatory variable) on spiderling body size at birth (i.e. carapace width). The polyandry status of mothers (i.e. the number of males observed mating with her), the male density treatment (ordered categorical variable) and the identity of the spider measurer were included as fixed factors. Field plot and female identity were included as random factors. Models were ranked from more to less parsimonious according to Akaike Information Criterion (AIC); ΔAIC = difference in AIC value relative to the best ranked model (Model 1). AICw, AIC weights; Cum. W, cumulative sum of AIC weights. (*) Significance values for the regression estimates

Nº	Model	AIC	ΔAIC	AICw	Cum. W
1	measurer**	-1322	0	0.725032205	0.72503221
2	null model**	-1320	2	0.266724442	0.99175665
3	measurer**; polyandry†	-1312	10	0.004885229	0.99664188
4	polyandry	-1311	11	0.002963041	0.99960492
5	male density‡	-1305	17	0.000147521	0.99975244
6	measurer**; male density	-1306	16	0.000243221	0.99999566
7	measurer**; male density; polyandry	-1297	25	2.70194E-06	0.99999836
8	male density; polyandry	-1296	26	1.63881E-06	1

* p<0.05; ** p<0.01
† Polyandry level (number of observed matings)
‡ Male density treatment (mothers)

Table A2. Generalized Linear Mixed Models on the effects of the polyandry treatment (ranking three levels: experimentally monandrous, voluntarily monandrous and polyandrous.) on spiderling body size for the 2006 field dataset. The cannibalistic treatment and measurer were included as fixed factors. Female identity was included as a random factor.

Nº	Model	AIC	ΔAIC	AICw	Cum. W
1	null model**	-2325	0	0.970493899	0.9704939
2	measurer*	-2318	7	0.029306376	0.99980027
3	polyandry†	-2308	17	0.000197465	0.99999774
4	cannibalism‡; polyandry	-2299	26	2.19364E-06	0.99999993
5	cannibalism; polyandry; measurer*	-2292	33	6.62421E-08	1
6	cannibalism x polyandry; measurer*	-2282	43	4.46336E-10	1

* p<0.05; ** p<0.01
† Polyandry treatment (mothers)
‡ Cannibalism treatment (mothers)

Table A3. Generalized Linear Mixed Models on the effects of polyandry on the growth rates of spiderlings in the 2005 season. The polyandry status of mothers (i.e. the number of males they mated) and both male density treatment (field) and feeding treatment (laboratory) were included as fixed factors. Field plot and female identity were included as random factors.

Nº	Model	AIC	ΔAIC	AICw	Cum. W
1	feeding‡ **	-3092	0	0.999998677	0.99999868
2	feeding **; male density†; polyandry	-3064	28	8.31528E-07	0.99999951
3	feeding x polyandry	-3062	30	3.05902E-07	0.99999981
4	feeding x male density	-3061	31	1.85539E-07	1
5	null model**	-2964	128	1.60381E-28	1
6	male density	-2949	143	8.87042E-32	1
7	polyandry	-2949	143	8.87042E-32	1

* p<0.05; ** p<0.01
† Male density treatment (mothers)
‡ feeding treatment (offspring)

Table A4. Generalized Linear Mixed Models on the effects of polyandry on the growth rates of spiderlings in the 2006 season. The cannibalistic and polyandry treatments along their interaction were included as fixed factors. Female identity was included as a random factor.

Nº	Model	AIC	ΔAIC	AICw	Cum. W
1	null model**	-289.3	0	0.984167616	0.98416762
2	cannibalism‡	-280.9	8.4	0.014758161	0.99892578
3	polyandry†	-275.6	13.7	0.001042682	0.99996846
4	cannibalism; polyandry	-268.6	20.7	3.14863E-05	0.99999995
5	cannibalism x polyandry	-255.9	33.4	5.49985E-08	1

* p<0.05; ** p<0.01
† Polyandry treatment (mothers)
‡ Cannibalism treatment (mothers)

Table A5. Cox Proportional Hazards Regression Mixed Models on survivorship of spiderlings in the 2005 season. The explanatory variable "time to death", combined both date of death and a censoring variable indicating spiderling death or survival by the end of the observation period. Field plot and female identity were included as random factors. NOTE.— coxme reports AIC values for improvement in fitting and in these analyses higher values mean a better fit.

Nº	Model	AIC (integrated)	AIC (penalized)
1	null model	85.9	119.0
2	feeding‡ x polyandry*	85.1	122.0
3	polyandry	83.9	118.7
4	male density†; feeding x polyandry*	83.3	121.7
5	feeding; polyandry	81.9	116.7
6	feeding; male density; polyandry	80.0	116.4

* p<0.05; ** p<0.01
† Male density treatment (mothers)
‡ Feeding treatment (offspring)

Table A6. Generalized Linear Mixed Models with binomial distribution on the number spiderlings which were found death and alive (explanatory variable) in field enclosures during the 2006 season. Both polyandry and cannibalistic treatments, the interaction between them and the initial spiderling density in the plots were included as fixed variables. Time since release was included as a covariate in the analyses to control for daily mortality due to differences in the beginning of each hatching replicate.

Nº	Model	AIC	ΔAIC	AICw	Cum. W
1	time since release*; density	147.2	0	0.382361	0.3823612
2	time since release*	148.5	1.29	0.200611	0.5829718
3	time since release; cannibalism‡	150.0	2.8	0.094289	0.6772609
4	time since release*; polyandry†	150.5	3.29	0.073801	0.7510614
5	time since release; polyandry x cannibalism; density*	151.2	4.01	0.051489	0.8025503
6	time since release; cannibalism; density x polyandry	151.6	4.43	0.041736	0.8442863
7	time since release; polyandry; density x cannibalism	151.6	4.46	0.046436	0.8907226
8	time since release; cannibalism; polyandry	152.80	3.43	0.072113	0.9628356
9	Null model**	152.6	5.45	0.025593	0.9884284
10	time since release; polyandry*cannibalism	153	5.83	0.020726	1.0091539

* p<0.05; ** p<0.01
† Polyandry treatment (mothers)
‡ Cannibalism treatment (mothers)

Table A7. Generalized Linear Mixed Models for the 2005 data set on the effects of polyandry on variability in spiderling body size at birth. The dependent variable was the standard deviation of spiderling carapace width (n=20 for each female). The male density treatment (ordered categorical variable), the polyandry status of mothers, the mean offspring size (i.e. mean spiderling carapace width for each female) and the identity of the spider measurer were all fixed factors in the models. Field plot was included as a random factor.

Nº	Model	AIC	ΔAIC	AICw	Cum. W
1	polyandry*	-236.2	0	0.630653027	0.63065303
2	male density†	-233.9	2.3	0.199687937	0.83034096
3	body size‡; polyandry*	-231.8	4.4	0.069878347	0.90021931
4	polyandry*; measurer*	-231.2	5	0.051767153	0.95198646
5	body size; male density	-229.9	6.3	0.027024824	0.97901129
6	male density; measurer*	-228.8	7.4	0.015591967	0.99460325
7	polyandry; male density	-225.9	10.3	0.003663785	0.99826704
8	body size; male density; polyandry	-221.7	12.2	0.001414931	0.99968197
9	male density; polyandry; measurer*	-220.9	15.3	0.000300226	0.9999822
10	body size; male density; polyandry; measurer*	-215.9	20.3	2.46434E-05	1.00000684

* p<0.05; ** p<0.01
† Male density treatment (mothers)
‡ Offspring carapace width

Table A8. Generalized Linear Mixed Models for the 2006 data set on the effects of polyandry on variability in spiderling body size at birth. The dependent variable was the standard deviation of spiderling carapace width (n=20 for each female). The explanatory variables included the cannibalistic and polyandry treatments, the measurer identity and the mean offspring size (i.e. carapace width).

Nº	Model	AIC	ΔAIC	AICw	Cum. W
1	null model**	-432.7	0	0.23775451	0.23775451
2	body size	-432.2	0.32	0.20260102	0.44035553
3	cannibalism‡	-431.5	1.07	0.13924551	0.57960104
4	measurer	-430.6	1.94	0.0901287	0.66972974
5	cannibalism x polyandry† *	-429.2	2.27	0.07641956	0.7461493
6	cannibalism; polyandry	-428.9	3.15	0.05817045	0.85503561
7	polyandry	-428.8	3.54	0.04326449	0.9535331
8	body size; cannibalism; polyandry	-428.4	3.14	0.055233	0.9102686
9	body size; cannibalism x polyandry	-427.9	3.09	0.05071586	0.79686516
10	measurer; cannibalism x polyandry *	-426.9	4.19	0.03031223	0.98384532
11	measurer; body size; cannibalism x polyandry	-425.6	5.05	0.01933708	1.0031824
12	measurer; body size; cannibalism; polyandry	-426	5.44	0.01566202	1.01884442

* p<0.05; ** p<0.01
† Polyandry treatment (mothers)
‡ Cannibalism treatment (mothers)

Table A9. Generalized Linear Mixed Models to test the diversifying bet-hedging hypothesis of polyandry on the variability in growth rates of spiderlings under two controlled feeding conditions. This data set correspond to offspring of mothers from the 2005 field experiment. The dependent variable was the standard deviation in growth rates (n=20 for each female). The fixed factors were the male density treatment (ordered categorical variable), the polyandry of mothers, spiderlings growth rate and laboratory feeding treatment (high vs low). Field plot and female identity were included as random factors.

Nº	Model	AIC	ΔAIC	AICw	Cum. W
1	null model**	-538.5	0	0.996092536	0.99609254
2	polyandry*	-527.3	11.2	0.003683414	0.99977595
3	feeding‡ **; polyandry*	-521.7	16.8	0.000223989	0.99999994
4	feeding x polyandry	-504.9	33.6	5.03677E-08	0.99999999
5	feeding x polyandry; growth rate§	-500.1	38.4	4.56926E-09	0.99999999
6	feeding; growth rate; male density†; polyandry*	-499.5	39	3.38499E-09	1
7	feeding x growth rate; male density; polyandry*	-493.4	45.1	1.60309E-10	1
8	feeding x polyandry; males	-487.4	39.9	2.15836E-09	1
9	feeding; growth rate; polyandry x male density	-484	54.5	1.45806E-12	1
10	feeding x male density; growth rate; polyandry*	-483.3	55.2	1.02748E-12	1

* p<0.05; ** p<0.01
† Male density treatment (mothers)
‡ Feeding treatment (offspring)
§ Change in spiderling carapace width during development in the laboratory

Table A10. Generalized Linear Mixed Models to test the diversifying bet-hedging hypothesis of polyandry through their effects on the variability in offspring growth rates in the 2006 season. The dependent variable was the standard deviation in growth rates (n=20 for each female). The fixed factors were both male density and polyandry treatments, and mean offspring growth rate was included as a covariate explaining between sibling variability. .

Nº	Model	AIC	ΔAIC	AICw	Cum. W
1	null model**	-102.5	0	0.606964052	0.606964052
2	growth rate§	-100.1	2.3973	0.183061025	0.790025077
3	cannibalism‡	-99.8	2.67511	0.159319969	0.949345046
4	polyandry †	-97.1	5.39413	0.040911229	0.990256275
5	polyandry; cannibalism	-94.1	8.37547	0.009214097	0.999470371
6	polyandry x cannibalism	-88.3	14.19895	0.000501072	0.999971443
7	polyandry x cannibalism; growth rate	-82.5	19.92868	2.85565E-05	1

* p<0.05; ** p<0.01
† Polyandry treatment (mothers)
‡ Cannibalism treatment (mothers)
§ Average change in carapace width per unit time during spiderlings dispersal in field plots

MANUSCRITO IV

Evolutionary stability of two animal behavioral types: the case of premating sexual cannibalism

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Resumen

Los síndromes comportamentales enfatizan como un tipo comportamental puede mejorar la eficacia biológica en algunas situaciones mientras que es perjudicial en otras. Un ejemplo ya clásico de síndrome comportamental es la hipótesis spillover del canibalismo sexual pre-cópula, según la cual las hembras que son genéticamente agresivas son favorecidas porque crecen a un tamaño mayor, lo que se traduce en una mayor fecundidad. Sin embargo, en el contexto sexual, estas hembras agresivas también atacan indiscriminadamente a los machos que se aproximan, a pesar de tener un mayor riesgo debido a la falta de fecundación si los machos son escasos. Aquí usamos un modelo basado en los individuos para determinar bajo qué escenarios ecológicos es más probable que prevalezca y evolucione esta estrategia spillover al compararla con otra estrategia donde las hembras atacan a los machos que se aproximan solo si antes se han apareado y asegurado el esperma para fertilizar sus huevos. Encontramos que una estrategia spillover pura nunca podría prevalecer sobre una estrategia de aparearse primero/canibalizar después (MFCL). Sin embargo, una variación de la estrategia spillover, la estrategia spillover temprana (EARLY-SPOV), donde las hembras se hacen adultas antes además de alcanzar un mayor tamaño (reflejando tasas de crecimiento más rápidas), podría mantenerse en algunos escenarios ecológicos e incluso invadir una población de hembras que siguen la estrategia MFCL. También encontramos que en algunos escenarios ecológicos ambas estrategias podrían coexistir a través de selección dependiente de frecuencia. Además, usando datos de los tiempos de maduración, las tasas de crecimiento y el canibalismo sexual en la araña lobo *Lycosa hispanica,* proporcionamos apoyo parcial a la predicción de que las dos estrategias pueden coexistir en una población natural. Nuestros resultados contribuyen a desvelar cómo evolucionan y se mantienen las personalidades animales en poblaciones naturales.

***Palabras clave**: Síndromes comportamentales, canibalismo sexual, agresión "spillover", Lycosa hispanica, modelos basado en los individuos, selección dependiente de frecuencia.*

Abstract

Behavioral syndromes emphasize how a type of behavior may enhance fitness in some situations while being detrimental in others, and may be central to understand the maintenance of behavioral variability in natural populations. One, now classic, example of behavioral syndrome is the spillover hypothesis of premating sexual cannibalism, in which genetically aggressive females are favored because they grow to a larger size and this translates into higher fecundity. However, in the sexual context, these aggressive females also attack approaching males indiscriminately, even at the risk of remaining unmated if males are scarce. Here we use an individual based model to determine the ecological scenarios under which this spillover strategy is more likely to prevail and evolve when compared to a strategy in which females attack approaching males only once the female has secured sperm via mating. We found that a pure spillover strategy could never prevail over a mate-first/cannibalize-later (MFCL) strategy. However, a variation of the spillover strategy, the early-spillover strategy (EARLY-SPOV), in which females become adults earlier in addition to reaching a larger size (reflecting faster growth rates), could be maintained in some ecological scenarios and even invade a population of females following the MFCL strategy. We also found that under some ecological scenarios both behavioral types could coexist through frequency-dependent selection. Additionally, using data of the burrowing wolf spider Lycosa hispanica on female maturation times, growth rates and sexual cannibalism we provide support to the prediction that the two strategies may coexist in a natural population. Our results clarify how animal personalities evolve and are maintained in natural populations.

***Keywords**: Behavioral syndromes, sexual cannibalism, spillover aggression, Lycosa hispanica, Individual Based Models (IBMs), frequency-dependent selection.*

Introduction

Behavioral syndromes, which are at the core of behavioral ecology (Sih et al. 2004a,b; Bell 2007; Sih et al. 2012), emphasize how individual behavior may be correlated over time or across situations, and that the adaptive value of one type of behavior (i.e. an individual's set of behavioral traits) may depend on the extent to which this is expressed across contexts. These constraints may have important ecological and evolutionary implications at different organization levels of animal systems (Pruitt et al., 2008; Pruitt et al., 2010) as, for instance, variability in the levels of behavioral plasticity could be constrained by the strength of correlations among traits leading to inter-individual differences in behavior (Reale et al. 2007; Reale et al. 2010).

Despite the cumulative evidence of behavioral syndromes, few models have attempted to investigate how they evolve and are maintained in natural populations and what selective agents may be responsible for their evolutionary establishment and/or extinction in populations. For instance, the model proposed by Fogarty et al. (2011) serves to explain sociality and invasion processes in species with variable aggressive phenotypes, in addition to explain the maintenance and evolution of behavioral syndromes involved in dispersal patterns of spiders in polymorphic populations (e.g. Kralj-Fišer and Schneider, 2012). Why are behavioral syndromes pervasive in some populations or species but are replaced by extensive behavioral plasticity in others? In particular, behavioral plasticity (or plastic personalities) may evolve and overcome the decrease in fitness caused by behavioral syndromes, allowing individuals to behave optimally in every behavioral context. However, despite setting constraints on behavioral plasticity (Sih et al. 2004a,b; Dingemanse et al. 2007; Sih et al. 2012), in some ecological scenarios a behavioral syndrome could be good enough that selection favoring plasticity could be very weak or negligible. However, escaping these constraints could be achieved by the evolution of adaptive flexible behaviour (Dingemanse et al. 2009; see also Dingemanse et al. 2010). Behavioral syndromes can therefore maintain the expression of non-optimal behaviors because they are adaptive in a single context in which the intensity of selection may be too high (e.g.

in a foraging context), despite being apparently maladaptive in the other contexts. However, there is still dissension about whether or not behavioral syndromes are potentially constraining behavioral evolution (Bell 2005; Dingemanse et al. 2007; Pruitt et al., 2008; Pruitt et al., 2010).

A now classic example of behavioral syndrome is sexual cannibalism; i.e., females killing and consuming males before, during or after mating (Elgar 1992; Elgar and Schneider 2004), which is a behavioral syndrome when (genetically-determined) female aggressive behavior towards prey is correlated to female aggressive behavior towards approaching males. This pre-mating sexual cannibalism (i.e., occurring before mating) *per se* would be a maladaptive by-product of selection favoring fast growth rates and thus voracity in females (Arnqvist and Henriksson 1997; Johnson and Sih 2005, 2007). In view of the "spillover hypothesis" (ASH hereafter), the propensity of the female to attack approaching males is genetically correlated with her voracity and this may lead to a female attacking a male even if it would be not adaptive for her (i.e. the SPOV strategy), like prior to insemination when she is still virgin, or regardless of her feeding status (i.e., hunger). In spiders, for instance, males may be limiting resources as sperm donors for females (Arnqvist and Henriksson 1997; Moya-Laraño et al. 2003a) and thus behaving in such a maladaptive way seems counterintuitive. However, this behavior may be a behavioral syndrome and not be completely maladaptive if the net selective effect of growing to a larger size (and thus producing more eggs) overcomes the risk of remaining unfertilized. Several studies in different spiders already provide support for the ASH, as they show correlations between female aggressiveness and their tendency to attack an approaching male (Riechert and Hedrick, 1993; Johnson and Sih 2005, 2007; Pruitt and Riechert 2009a; Pruitt et al. 2008; Pruitt et al. 2011b; Rabaneda-Bueno et al. 2014). In particular, in the fishing spider *Dolomedes triton* Johnson and Sih (2005, 2007) reported that 1) voracity towards heterospecific prey was correlated with juvenile feeding rate, adult female size and fecundity, 2) juvenile and adult voracity are positively correlated, 3) voracity towards heterospecific prey is positively correlated with pre-copulatory sexual cannibalism and 4) even though there is some plasticity to tune down boldness in the presence of predators depending on

the benefit of the context in which boldness is expressed, individual differences in boldness are maintained and correlated across contexts regardless of predation threat.

Alternatively, sexual cannibalism may occur differently (Newman and Elgar 1991; Elgar 1992) if females evolved behavioral flexibility and despite high levels of voracity during their young stages they were able to adjust their attacks to males depending on whether the female is hungry (Moya-Laraño et al. 2003b; Barry et al. 2008; Wilder and Rypstra 2008) or the female has previously mated (Johnson 2001; Erez et al. 2005; Rabaneda-Bueno et al. 2008). Females that behave according to the latter pattern would follow what we call the "mate first and cannibalize later" strategy (MFCL). Thus, the MFCL strategy would not be a behavioral syndrome in the sense that female behavior at the adult stage may be decoupled from that at her younger life, but rather a plastic behavioral type. An alternative view of the MFCL strategy is that females are able to discriminate males from other prey and tune down their aggressive behavior selectively towards the former. An important difference between the MFCL and the SPOV strategies is that in the former feeding on males greatly improves female fitness (Newman and Elgar 1991; e.g. Rabaneda-Bueno et al. 2008), whereas in the latter adult feeding would not explain differences in female fecundity (Arnqvist and Henriksson 1997). However, the study by Johnson and Sih (2005) suggests that the view of the SPOV strategy could be expanded to include the fitness consequences of foraging on female fecundity.

Several studies have already related behavioral types with specific fitness outcomes (Dingemanse et al. 2004; Dingemanse and Reale 2005). In the case of sexual cannibalism, if we focus on bold and aggressive traits, consistent individual differences across different ecological contexts should be apparent through their effects on the fitness of SPOV and MFCL females. For instance, when acting as prey, due to the heavy impact of predation on population density (Moya-Laraño 2002; Moya-Laraño et al. 2003a; Rabaneda-Bueno et al. 2008), SPOV females (i.e. bolder and active foragers) would be expected to suffer higher death rates than the more cautious MFCL females. Moreover, aggressive spiders may be more likely to attack potentially dangerous predators (e.g., other females Moya-Laraño et al. 2002)

further increasing the costs of a SPOV strategy. Hence, this could generate mortality patterns dependent on SPOV and MFCL frequencies, and differential selective pressures and trade-offs between personality traits and fitness outcomes in different ecological contexts (e.g. Johnson and Sih, 2005; Biro et al., 2006; Pruitt and Riechert, 2009a). These context dependent trade-offs can ultimately be crucial to maintain genetic variation in behavioral types. Individual based models (IBMs) are computer simulations that are implemented to address ecological and evolutionary questions (DeAngelis and Mooij 2005; Grimm et al. 2006). In these simulations the fate of different individuals is monitored within generations and under different ecological scenarios and, in evolutionary questions, one can study the fate of alleles across generations (evolutionary dynamics). Here we investigate under which ecological scenarios would the SPOV or MFCL strategies evolve and be maintained by building an IBM (Ungoliant 1.0) in which both strategies can potentially invade the same population and by contrasting the occurrence and timing (generation) of invasion of one or another strategy in different environments (i.e. productively rich and productively poor). To tentatively test whether the strategies predicted to be evolutionarily stable do actually coexist in a natural population, we also analyzed data from field experiments (Rabaneda-Bueno et al. 2008; 2014) on sexual cannibalism in the burrowing wolf spider *Lycosa hispanica* (formerly *L. tarantula*).

Materials and Methods

The model

Model assumptions

Some of the most important model assumptions in the model are the following:

1 – The population is closed to migration.

2 – The population is near carrying capacity and thus there is no population growth across generations. Thus, we set a constant number of adult individuals (N = 1000) each generation and assume that eco-evolutionary dynamics is negligible.

3 – Female feeding status does not affect the timing of oviposition and fitness is not enhanced by early oviposition (but see Rabaneda-Buento et al. 2008)
4 – The level of aggression is determined by a single sex-linked locus. For implementation we considered sex determination of spiders to come from a XX (females)-X0 (males) system (Král et al. 2006).
6 – Males are pure carriers for the alleles of aggression and for simplicity they are all phenotypically identical.
7 – There is no male or female choice (but see Rabaneda-Bueno et al. 2014). Previous residency at female burrows determines which male stays and cohabits with the female (Fernández-Montraveta & Ortega 1993; Elgar 1998).
8 – Females mate only once and are never sperm limited.
9 – There is no explicit space and individuals encounter each other randomly.
10 – All eggs are of equal size and egg size does not affect offspring quality.
11 – As females are territorial (Moya-Laraño et al. 2002), competition for prey are negligible.
12 – Post-mating sexual cannibalism is negligible (Moya-Laraño et al. 2003a; Rabaneda-Bueno et al. 2008).

Model algorithm

Fig. 1 shows the flow diagram for the model's algorithm. Each season, we simulated hundreds of males and females who encountered each other randomly each day. Depending on a sex-linked strategy (SPOV or MFCL), a female will be more or less prone to attack an approaching male. At the end of each season, females that remain alive and who have successfully mated, produce an egg sac which will contribute to the genetic pool of the next generation. If no single strategy takes over the population (coexistence), the simulation stops after 20,000 generations. Based on published data, we also set a 1:1 sex ratio at maturation and thus 500 males and 500 females reached maturity each generation (Orta et al. 1993) , as for most solitary spiders in temperate environments (Uhl and Gunnarsson 2001). A feeding algorithm allowed each female spider to increase her condition (abdomen width) each day by a factor which dependent on the strategy and on the environment (see Environments below), simulating foraging

encounters. The model was written in MATLAB and a copy of the code can be found at: http://www.eeza.csic.es/foodweb/Simulators_FWEE.html

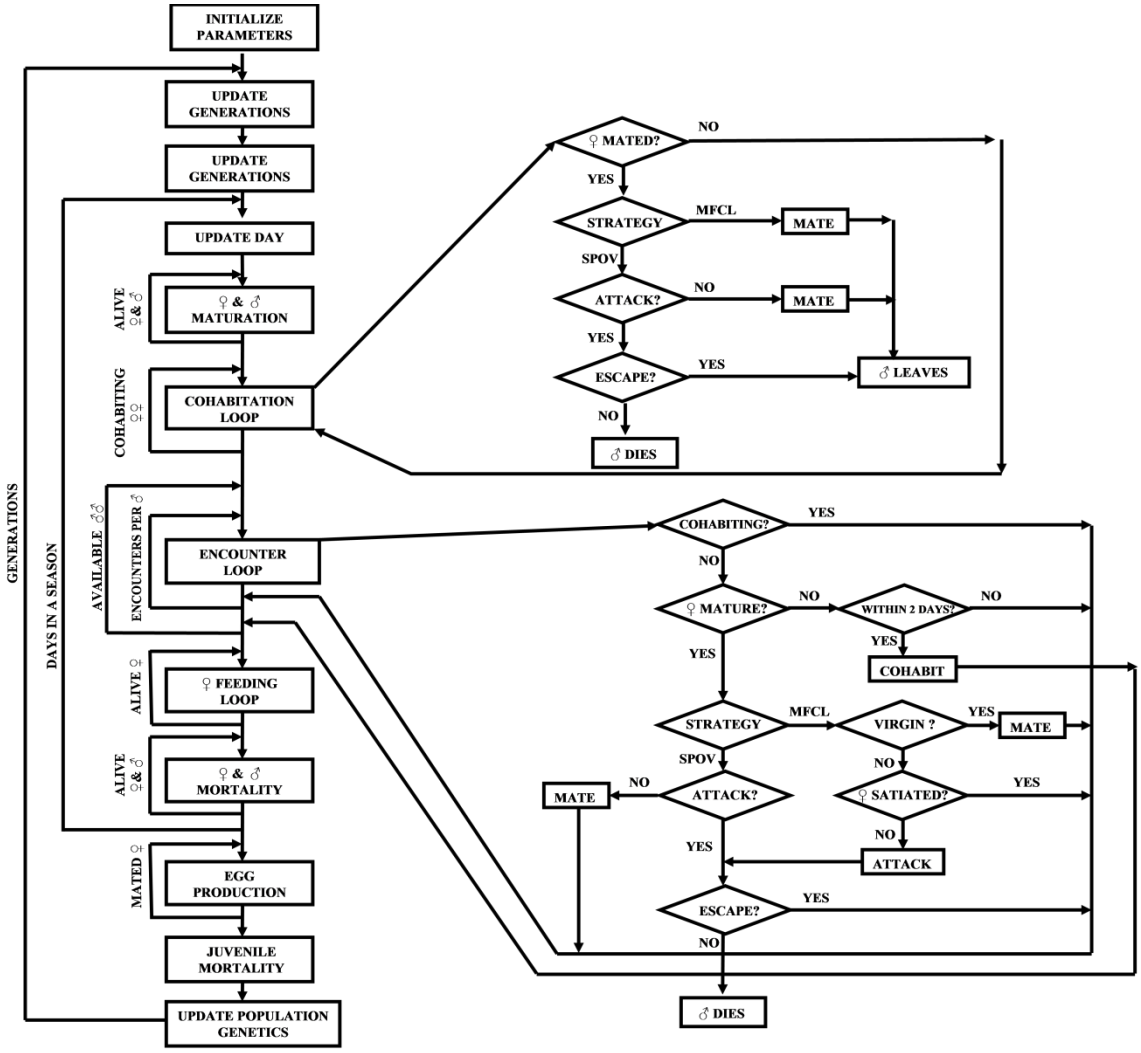

Fig. 1. Model flow diagram. Each day (encounter loop starting in the center of the diagram and flowing to the right) a male randomly encounters a number of females whose genotypes determine their cannibalistic strategy (MFCL or SPOV). SPOV females attack the males regardless of whether females have previously mated or have reached satiation. MFCL females attack males only if these females have previously mated or if they are not satiated. Males have some probability of escaping a female attack. Males may expend a few days cohabiting (top right loop) with virgin females (Moya-Laraño et al. 2003a; Moya-Laraño et al. 2004), and each day males have a probability of mating or being attacked by this female, which will also depend upon the female strategy. Each day females feed on alternative prey, depending on strategy (SPOV feeding at a higher rate than MFCL). Associated mortality rates for males and femalesdepend upon strategy (SPOV higher mortality rates than MFCL). At the end of the mating season, females reproduce according to their strategy, with offspring mortality also contingent on the strategy (SPOV higher mortality than MFCL). See text and Table 1 for further details and model parameterization.

Model parameterization

Field parameters of the Iberian tarantula (Lycosa hispanica). Other than the values of the parameters that were combined in the simulations in order to uncover which ecological scenarios favor one or another strategy, most fixed parameters in the model came from field data on the Iberian tarantula (*Lycosa hispanica*, formerly *L. tarantula*), a burrowing wolf spider (Table 1).

Body condition and food intake. As the data available for parameterization were morphological and females were not actually weighed in the field in any of the studies available, body condition and its increments from foraging, was incorporated in the model as abdomen width (in mm). To truly estimate mass from abdomen width one would need the density of the nutrients stored in the abdomen as well (Moya-Laraño et al. 2008), and this information is not available. Since we have the necessary equations relating abdomen width with reproductive output (Table 1), using abdomen width was both simpler and easier.

Strategies and alleles. In order to include the correlational effect of the sexual cannibalism behavioral syndrome across contexts, SPOV individuals and those with related strategies, experienced relative to MFCL, both higher food intake during the adult stage (higher rapaciousness), higher mortality during both the young and adult stages (higher exposure to predators from higher foraging activity and boldness, e.g., Higgins and Rankin 2001; Moya-Laraño 2002; Moya-Laraño et al. 2003b; Sih et al. 2004a,b) and they had a higher propensity to attack approaching males during the mating season (Table 1). The latter fact was considered in the model by the parameter "pspov" which determined the probability that a SPOV female of attacked an approaching male. Males could then escape with a proability which depended on female size (Table 1). To accommodate realistic sizes/age at maturity relationships, female fixed body size (carapace width, CW) was determined by its relationship with maturation time. To include realistically large SPOV in the simulations, the slope of the relationship was steeper for SPOV than for. Furthermore, although not explicitly noted in the verbal model of Arnqvist and Henriksson (1997), higher voracity and its associated higher growth rate could translate into early maturation, in addition to larger size (Uetz 1992; Prokov and Václav 2008). Thus, we additionally included this fact in

our implementation of the SPOV strategy, and added a strategy called EARLY-SPOV, in which females matured earlier and to a larger size, for which we shortened maturation time of EARLY-SPOV relative to MFCL by 30%.

In the original Arnqvist and Henriksson (1997) verbal model, most of the variation in female fecundity was hypothesized to be due to her fixed size at maturation, measured as her carapace dimensions (modern –Araneomorphae-spiders do not molt after reaching the adult instar), and thus sexual cannibalism would have little effect on female fecundity. However, this idea counters to recent findings in cursorial spiders, in which adult feeding (and thus body condition before egg-laying – mass relative to fixed size) has been found to also determine part, if not most, of the variation in female fecundity (Moya-Laraño 2002; Johnson and Sih 2005). Thus, we also tested Condition-Dependent SPOV (CD-SPOV) and Condition-Dependent EARLY-SPOV (CD-EM-EARLY-SPOV) females, in which their foraging success during their adult life also contributed to explain their fecundity (Table 1). For simplicity, throughout we refer to all these strategies related to the spillover hypothesis simply as SPOV.

Rather than simulating all juvenile life-stages, we simplified juvenile life by a single parameter "different", which settled which proportion of SPOV juveniles survived to the adult stage. In principle, the more voracious juveniles (with SPOV phenotype) should experience higher mortality rates and accrue more food (Arnqvist and Henriksson 1997; Johnson and Sih 2005). However, higher foraging success should allow them to grow faster to a faster rate, making them to have, at the very least, a size cannibalistic advantage (e.g. Samu et al. 1999; Rabaneda-Bueno et la. 2008) over small slow-growing MFCL juveniles. Thus, the parameter "different" measures the balance between the cost and the benefit for SPOV juveniles to be more rapacious. Since the actual balance may actually depend on predator pressure, which may largely vary across environments, we simulated a large array of "different" values (Table 1).

Environments. We considered two distinct environments (poor and rich). A poor environment is characterized by having low food availability, and at least in spiders, a lower density of individuals (Wise 1993), which in turn will mean a lower rate of encounter between the sexes. Thus, in poor environments, the

maximum number of encounters per day for a male ("maxenc") was low (1) and high in rich environments (3). Also, in poor environments the daily increase in condition was half of that in rich environments (Table 1). Poor environments also considered higher predation mortality of adult SPOV relative to adult MFCL females; as well as SPOV females attacking approaching males at a higher rate (Table 1).

Simulations

We ran two main sets of simulations. In the first set, we were interested in knowing under which ecological scenarios one or another strategy would be maintained in populations. The second set of simulations was devised to study under which ecological scenarios a new mutation determining one strategy could invade a population dominated by the other strategy. The simulations on maintenance actually served to pick a meaningful set of parameters that could be used to study the evolution of strategies.

To study the scenarios for the maintenance of the two strategies, we started with a 50% frequency for each of the alleles. We ran all these simulations twice, once considering SPOV (33% *Sm*, 33% *SS* and 33% *mm*) as genetically dominant and another considering MFCL as dominant (33% *sM*, 33% *MM* and 33% *ss*).

We then ran almost identical simulations as the ones before but with SPOV allele frequencies taking values of either 0.01 or 0.99, emulating a novel mutation arising in a population of pure MFCL or in a population of pure EARLY-SPOV respectively (SPOV *vs*. MFCL was not investigated because further we found that SPOV was never maintained when confronted with MFCL). The aim of these simulations was to reveal under which ecological scenarios one new mutation could invade the other. Sensitivity analyses, including a wider range of parameters than those on Table 1, allowed testing the robustness of our conclusions (Electronic Appendix).

Field data: do the simulated strategies coexist in the wild?

The data used here come from a field experiment on the burrowing wolf spider *L. hispanica*, the results of which have been already published (Rabaneda-Bueno et al. 2008; 2014) or are part of another ms (Rabaneda-Bueno et al., *in prep*). Importantly, these data were gathered after most of the simulations had been run, and therefore the model was never motivated by the data but *viceversa*. We here briefly mention the methods to allow an easier interpretation of the results. In a field common garden in which each female received natural prey *ad libitum*, eighty females were offered a total of 199 males. Half of the females were assigned to a monandry treatment and received males only until they first mated and half of the females were assigned to a polyandry treatment and received three additional males after the female first mated. All males were used only once and offered sequentially (in different days) to the females. We recorded whether the female mated with the male or decided to attack and kill him, or whether none of the above occurred because the male remained frozen at the female burrow's mouth. We have previously successfully documented that there is a continuum of female rates of weight gain (Rabaneda-Bueno et al. 2014), reflecting a continuum in voracity rates in our common garden, further supported by the positive relationship between the female rate of weight gain (from maturation to the time a female first mated) and the probability that the female attacks the male. This result is consistent with the existence of spiders following a classic SPOV strategy (Arnqvist and Henriksson 1997) and others following a more docile strategy (low voracity and low propensity to attack males before the female mates) in a natural population of *L. hispanica*. However, since a purely SPOV strategy seems unlikely to be evolutionarily stable in the wild (this paper), here, we further analyzed the data collected during the above experiment to test whether an EARLY-SPOV strategy (much more likely to be evolutionarily stable in populations) could be present in the studied population. In particular, we tested the hypothesis that females maturing earlier would tend to gain weight at a higher rate in the period between maturation and first mating, which would be indicative of early-maturing females being more voracious. Note that this would not be an artifact of differences in food availability but a simple consequence of female behavior as natural prey were

equally provided *ad libitum* to all females in a common-garden experiment (Rabaneda-Bueno et al. 2008; 2014). In addition, these differences in female behavior were not a consequence of early-maturing females maturing earlier but hungrier either, as maturation time was negatively correlated with body condition at maturation (linear model on cubic root body mass and carapace width as covariate –Moya-Laraño et al. 2008-; molting date, b = -0.0004, t_{78} = -2.36, P = 0.021; carapace width; , b = 0.1243, t_{78} = 22.77, P < 0.0001), which means that early-maturing females were less no more hungry than late-maturing females. Despite the low number of females that cannibalized males before the female mated (N=8; Rabaneda-Bueno et al. 2008; 2014) we were able to test some additional patterns which help to support the hypothesis that two sexually-cannibalistic strategies may coexist in the wild. Data were analyzed using Generalized Linear Models with likelihood ratio tests and, depending on the nature of the data, either Normal or Binomial errors.

Results

Ecological scenarios for the maintenance of strategies

The MFCL strategy always persisted in populations when contrasted against the pure SPOV strategy. The SPOV allele went from a frequency of 0.5 to extinction in 4 to 66 generations depending on the combination of parameters (trajectories not shown). When a Condition-Dependent SPOV strategy (feeding affects female fecundity) was contrasted against MFCL, the results were qualitatively the same (Electronic Appendix).

However, when we contrasted a more realistic EARLY-SPOV strategy against the MFCL strategy, we found more variation in which strategy prevailed (Fig. 2). First, when the EARLY-SPOV allele was recessive (Fig. 2a), it fixated in the population in 4 out of 10 parameter combinations. Fixation of EARLY-SPOV occurred more likely in rich environments (3 out of 4 cases) and when the relative mortality of EARLY-SPOV juveniles was small. As expected, the higher the mortality of juvenile EARLY-SPOV, the lower the probability of persistence for this

strategy. When a Condition-Dependent EARLY-SPOV strategy (feeding affects female fecundity) was contrasted against MFCL, the results were qualitatively the same (Electronic Appendix).

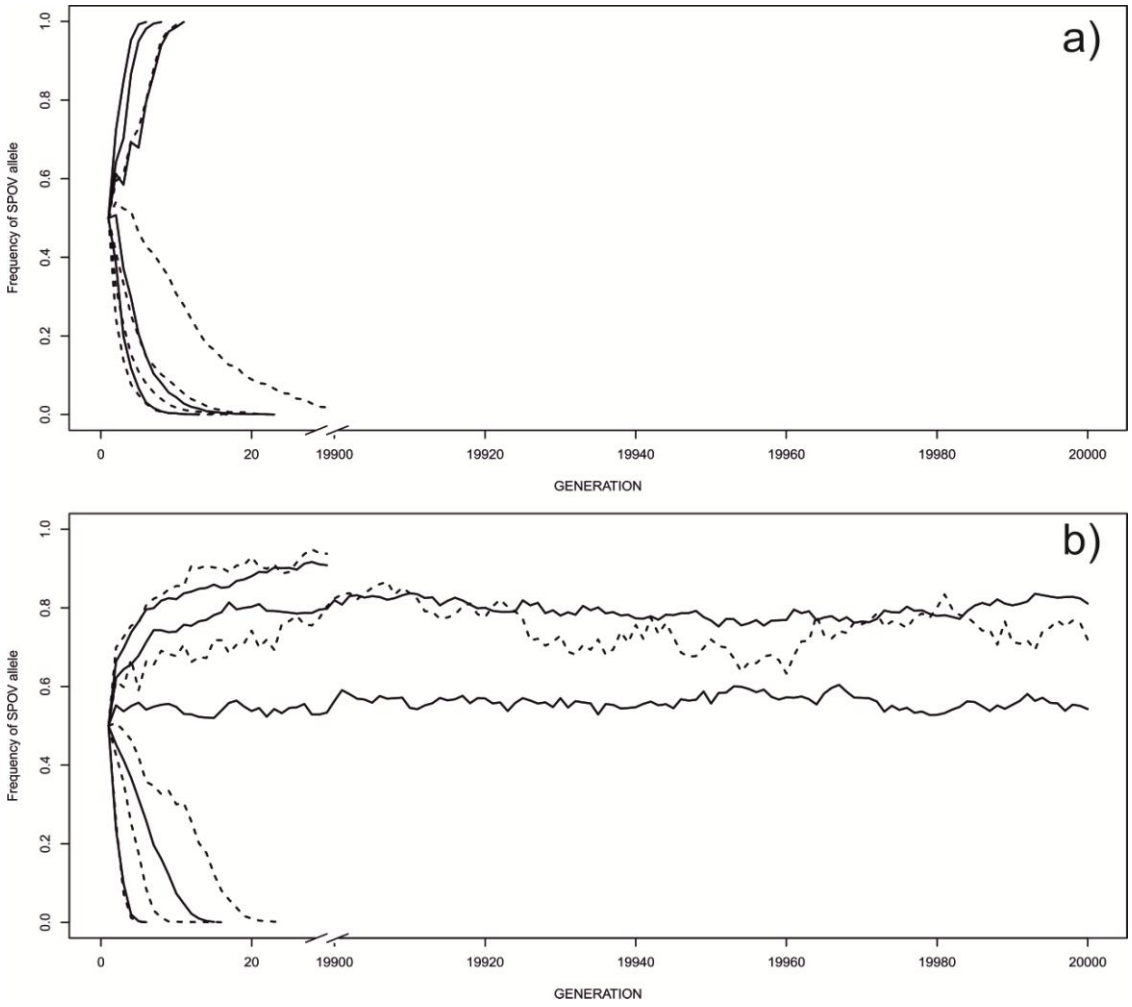

Fig. 2. Maintenance of either the EARLY-SPOV or the MFCL strategies depending on the type of environment. The Y-axis shows the frequency of the EARLY-SPOV allele (p) relative to the MFCL allele (q=1-p). Thus, zero frequency for EARLY-SPOV means 100% presence of MFCL. From bottom to top, and within each habitat type (rich or poor, respectively depicted by solid and dashed lines), the parameter "different" takes the values 0.1, 0.3, 0.5, 0.7 and 0.9 (A value of 0.5 means that 50 juveniles of the born EARLY-SPOV survive until maturation, and that 100% of MFCL survive). a) Allele dynamics when EARLY-SPOV is recessive; b) Allele dynamics when EARLY-SPOV is dominant (the arrows indicate points of extinction for the MFCL allele). Note the frequency-dependent equilibria that allow both alleles to persist in populations for thousands of generations. The two top curves interrupted at the break are two quasi-equilibria in which the MFCL strategy was eventually driven to extinction before generation 19900.

Frequency-dependent equilibria. Interestingly, when the EARLY-SPOV allele was dominant, we found 3 parameter combinations that resulted in frequency-dependent selection equilibria -with both strategies being maintained up until

generation 20,000- and two quasi-equilibrium, in which the MFCL allele disappeared before 19,900. In order to understand the nature of these equilibria we took the equilibrium that had the widest oscillation (different=0.7 for poor environments in Fig. 2b which had a frequency of the EARLY-SPOV allele ranging from 0.58 to 0.98 across the 20,000 generations) and divided the equilibrium according to the frequency of the EARLY-SPOV allele (i.e., BOTTOM: allele frequency<0.85 and TOP: allele frequency>0.85) and compared the fitness of individuals phenotypically following each strategy in the generations when the EARLY-SPOV allele was close to fixation (frequency>0.85) *vs*. the fitness of each strategy in all other generations (frequency<0.85). We performed GLMs with likelihood ratio tests (R core development team 2014) in which each data point was one generation. The dependent variable was an estimate of either EARLY-SPOV or MFCL relative fitness. We included position in the equilibrium (TOP or BOTTOM) as the main factor. Generation number was included as a continuous variable to control for temporal autocorrelation. We found that, once controlled for EARLY-SPOV frequency by including the frequency of the EARLY-SPOV allele as a covariate in the model, a higher percentage of MFCL females mated (χ_1^2 = 49.84; P < 0.0001) at the TOP position of the equilibrium (when EARLY-SPOV was close to fixation: least squares means ± SE, TOP: 7.67% ± 0.33; BOTTOM, 5.21% ± 0.09) and EARLY-SPOV females had lower relative fitness (estimated as the ratio between the mean number of EARLY-SPOV females surviving to maturation and the average between EARLY-SPOV and MFCL females surviving to adulthood) at the TOP position (1.70 ± 0.01) than at the BOTTOM position (1.81 ± 0.00, χ_1^2 = 85.4; P < 0.0001), consistent with the existence of a frequency-dependent equilibrium.

The evolution of strategies – the invasion of novel mutations

When EARLY-SPOV was almost the only strategy present in populations (initial allele frequency of 0.99) and its allele dominant, MFCL could invade in a wide range of ecological scenarios (Fig. 3), also sometimes originating frequency-dependent equilibria. MFCL females were much more likely to invade in relatively rich environments.

When MFCL was almost the only strategy present in populations (initial allele frequency of 0.99), however, EARLY-SPOV was able to invade only in one scenario: dominant EARLY-SPOV, rich environments and with the lowest possible juvenile EARLY-SPOV mortality (Fig. 4). Invasion occurred rather slowly and after a quasi-equilibrium in which both strategies coexisted for almost 2000 generations.

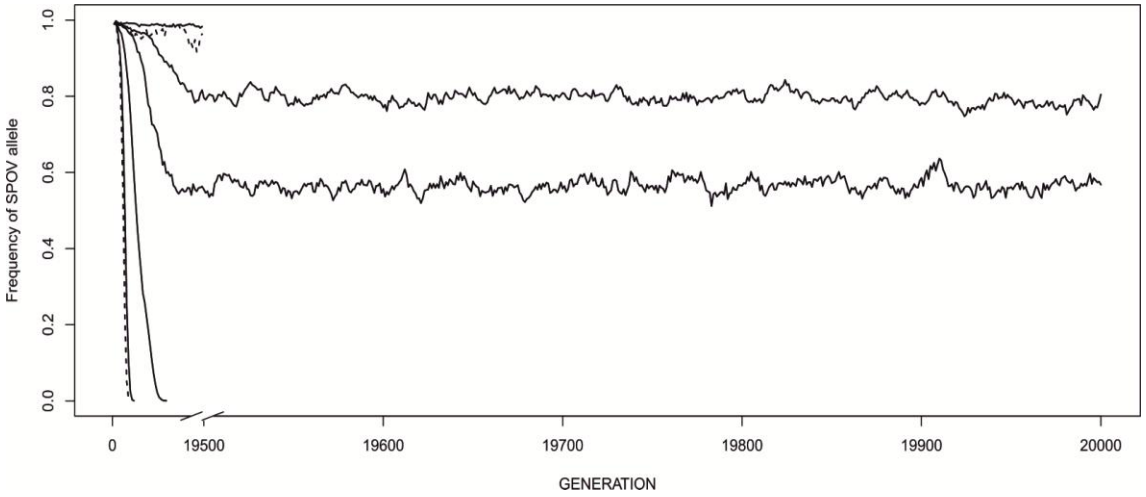

Fig. 3. Patterns of invasion of the MFCL strategy in a population in which 99% of individuals are EARLY-SPOV. The Y-axis shows the frequency of the EARLY-SPOV allele (p) relative to the MFCL allele (q=1-p). Thus, zero frequency for EARLY-SPOV means 100% presence of MFCL. From bottom to top, and within each habitat type (rich or poor, respectively depicted by solid and dashed lines), the parameter "different" takes the values 0.1, 0.3, 0.5, 0.7 and 0.9 (A value of 0.5 means that 50 out of 100 EARLY-SPOV born juveniles survive until maturation, and that 100% of MFCL survive). The two top curves interrupted at the break are two quasi-equilibria in which the MFCL strategy was eventually driven to extinction before generation 19500.

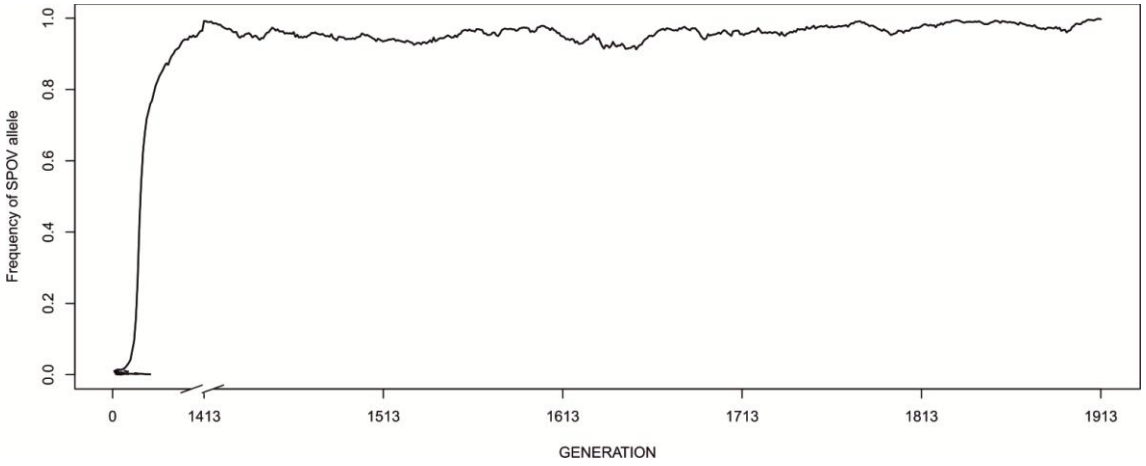

Fig. 4. Patterns of invasion of the EARLY-SPOV strategy in a population in which 99% of individuals are MFCL. The Y-axis shows the frequency of the EARLY-SPOV allele (p) relative to the MFCL allele (q=1-p). Thus, zero frequency for EARLY-SPOV means 100% presence of MFCL. The MFCL strategy prevails in all scenarios but one: rich environment with parameter "different" taking the value 0.9 (meaning that 90 out of each 100 born juveniles of EARLY-SPOV survive until maturation).

Detailed sensitivity analyses (Electronic Appendix) showed that the maintenance of EARLY-SPOV depended mostly on the encounter rates between males and females, being this strategy more likely to be maintained when encounter rates were higher. In addition, we found that allowing SPOV and EARLY-SPOV females to use the energy accrued as adults for offspring production (CD-SPOV and CD-EM-SPOV) did not change the results qualitatively as compared with SPOV and EARLY-SPOV respectively, indicating that the timing of maturation rather than fecundity is what confers an advantage to the SPOV strategy. Also, relatively low aggression levels towards males in EARLY-SPOV were less likely to allow this strategy to prevail in populations, Finally, increasing prey availability in a poor environment also allowed MFCL to exclude EARLY-SPOV when the juvenile mortality of the latter was lowest and the EARLY-SPOV allele dominant.

Field data: do the simulated strategies coexist in the wild?

We found that, prior to mating, there was a negative correlation between the timing of maturation (independent variable) and the rate of weight gain in the period after maturing and before mating (GLM, b = -888.9, t_{78} = -5.71, $P < 0.0001$; Fig. 5), reflecting differences in voracity between early- and late-maturing females, consistent with the existence of EARLY-SPOV and MFCL females in the population. Further, by dividing females in those that gained weight and those that lost weight before mating, we found that the ones gaining weight after maturing and prior to mating had matured 20 days earlier than those that lost weight during the same life stage (GLM, likelihood ratio test, $\chi_1^2 = 25.8$, $P < 0.0001$, Fig. 6), a figure that is very close to our simulated maturation differences between EARLY-SPOV and MFCL females of 17 days. However, the spiders that lost weight before mating compensated their relative losses by switching to a much higher rate of food acquisition after mating relative to those that gained weight at a high rate prior to mating (GLM on the difference between the rate of weight gain after first mating minus the rate of weight gain before first mating, likelihood ratio test, $\chi_1^2 = 82.2$, $P < 0.0001$, Fig. 7).

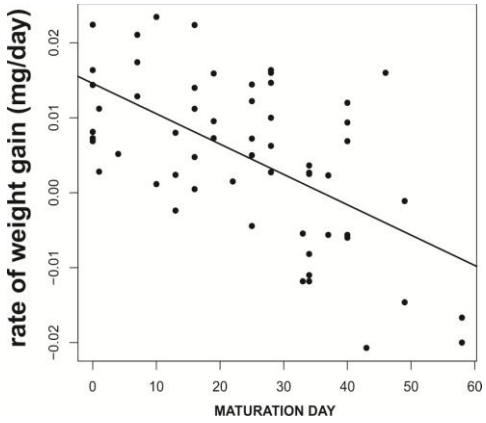

Fig. 5. Negative relationship between female age at maturation and the rate of weight gain after maturation. Data correspond to the burrowing wolf spider *L. hispanica* (Rabaneda-Bueno et al. 2008; 2014).

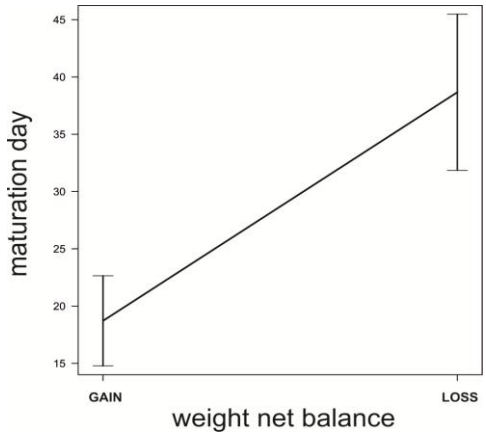

Fig. 6. Differences in molting dates between females that lost weight before her first mating and those that gained weight (and were clearly actively foraging) before her first mating took place. Data belong to the burrowing wolf spider *L. hispanica* (Rabaneda-Bueno et al. 2008; 2014).

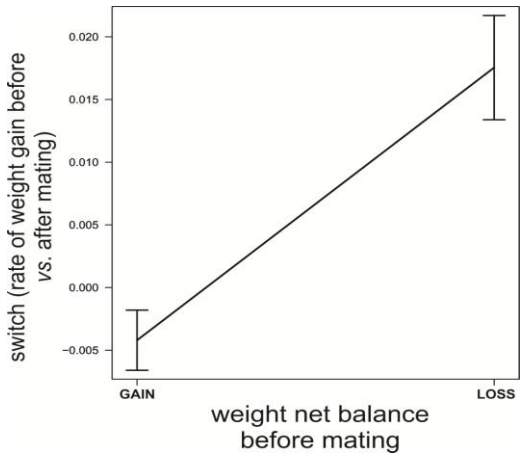

Fig. 7. Differences in switching in the rate of food acquisition (difference before vs. after first mating) between females that lost weight before her first mating and those that gained weight (and were clearly actively foraging) before her first mating took place. Data belong to the burrowing wolf spider L. hispanica (Rabaneda-Bueno et al. 2008; 2014).

In light of these results, we propose that both the magnitude of switching and the timing of maturation can indicate whether a female is closer to an MFCL or to an EARLY-SPOV strategist. Early-maturing females with low switching rates (i.e., indicating that they cannot modulate their foraging rate across contexts, before *vs*. after first mating) would be closer to EARLY-SPOV, whereas late-maturing females with high switching rates would be closer to MFCL females. Note, however, that this type of MFCL females would be slightly different than the MFCL females that have been modeled in our simulations, as in our data, and due to their flexible behavior, MFCL females would be able to compensate their relatively low feeding rates before mating by switching to higher feeding rates after mating (i.e., adaptive plasticity). Further compensation for the former relatively low rate of food acquisition may be achieved by feeding on any additional male that approaches a female after she has mated (Rabaneda-Bueno et al. 2008). To further confirm the above we classified the females that were offered additional males after mating as early cannibals if they had attacked a male before first mating (EARLY-SPOV), as late cannibals if they had attacked a male after first mating with another (MFCL) and as neutral if they had never attacked a male. We predicted that if early cannibals were consistent with an EARLY-SPOV strategy they should not switch their rates of weight gain between contexts (before *vs.* after mating) and clearly less than late cannibals. The latter, to be consistent in turn with a behaviorally-plastic MFCL strategy they could compensate previous mass losses during the period in which they were waiting to mate by switching to a higher rate of weight gain after first mating. Indeed, while early cannibals had a switching value near zero (i.e., they maintain an equal rate of weight gain before and after mating), late cannibals had a significantly higher switch value than early cannibals (GLM, $\chi_1^2 = 5.1$, $P = 0.024$, Fig. 8). Hence, after first mating, switching to a higher rate of attacks towards males correlated with a higher rate of weight gain (not explained by feeding on the attacked males as they were removed immediately from their mouths parts – Rabaneda-Bueno et al. 2008, 2014) and therefore of attacks to heterospecific prey, while females that cannibalized males before mating maintained a constant rate of weight gain (voracity) across contexts, consistent respectively with the coexistence of MFCL and EARLY-SPOV strategies in the population. Interestingly, 6 out of the 17 females consistent with the MFCL

strategy (those that killed a male only after mating) and 0 out of the 7 females consistent with the EARLY-SPOV strategy lost weight before mating respectively (Likelihood-ratio test, $\chi_1^2 = 4.92$, $P = 0.027$), suggesting that MFCL females may even stop feeding while waiting to mate with a male. Therefore, MFCL females could potentially be using adaptive plasticity, stopping feeding until a suitable male arrives and then immediately switching to be highly voracious right after mating. If that were the case, we could further detect the presence of MFCL females if those females that switch to a high voracity after mating are more likely to kill subsequent approaching males (i.e.; these would be the females that are docile and mate first, and that once mated they turn voracious and cannibalize subsequent approaching males latter). Such relationship was found in our data (binomial GLMM with female as random factor, $\chi_1^2 = 4.88$, $P = 0.027$, Fig. 9). Furthermore, to further confirm that the degree of switching may be an indication of the female strategy, females switching to higher feeding rates after first mating were the ones that also matured later, consistent with the MFCL strategy (GLM, $\chi_1^2 = 8.6$, $P = 0.003$, Fig. 10).

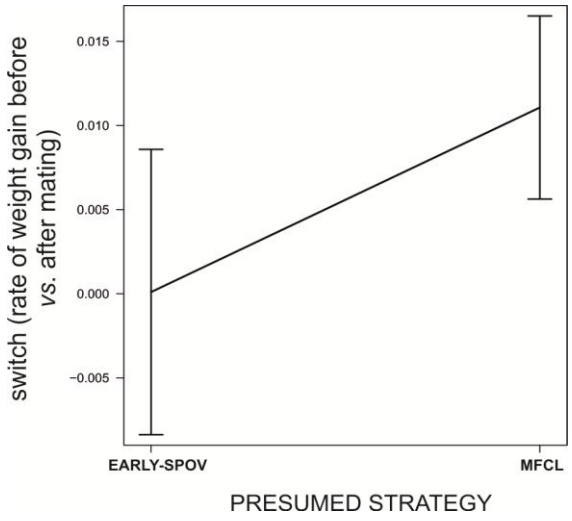

Fig. 8. Differences in switching in the rate of food acquisition (difference before *vs*. after first mating) between females that killed a male before the female had first mated (presumed EARLY-SPOV) and females that killed their first male after the female first mated (presumed MFCL). Data belong to the burrowing wolf spider *L. hispanica* (Rabaneda-Bueno et al. 2008; 2014).

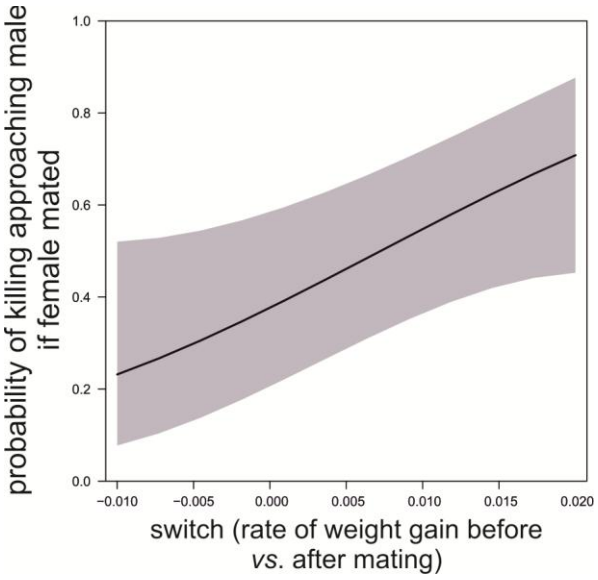

Fig. 9. Probability of females killing males that approach females one the latter have mated as a function of switching in the rate of food acquisition (difference before *vs*. after first mating).

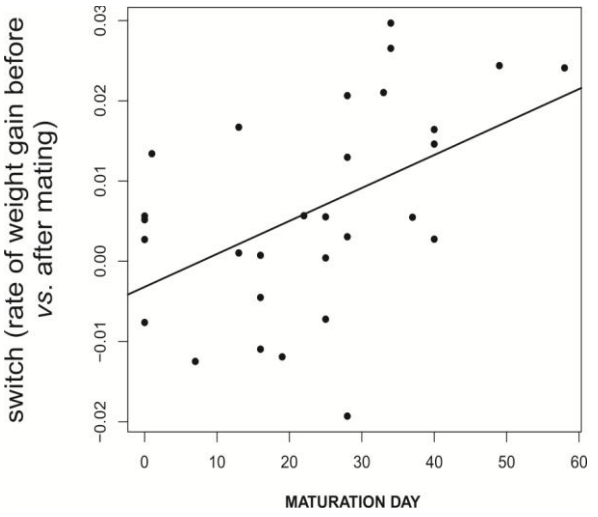

Fig. 10. Females that mature later have a higher switching rate of food acquisition (difference before *vs*. after first mating), as expected if they followed the MFCL strategy.

Discussion

We found that in natural populations, an adaptive strategy in which a female does not kill and/or consume males until she has obtained sperm (Newman & Elgar 1991; Elgar 1992; Rabaneda-Bueno et al. 2008)–our Mate First and Cannibalize Later strategy-will prevail over a pure spillover strategy (Arnqvist and Henriksson 1997; Johnson and Sih 2005, 2007) unless spillover females are unrealistically large. However, a spillover strategy in which higher levels of aggression against heterospecific prey lead to higher growth rates and larger, earlier-maturing adults resulted in a wide range of scenarios in which this EARLY-SPOV strategy could be maintained in natural populations instead of the MFCL strategy. We even found ecological scenarios in which this EARLY-SPOV strategy could invade the previously prevailing MFCL strategy over evolutionary time. However, the MFCL strategy was able to prevail and to invade the EARLY-SPOV strategy in the majority of ecological scenarios. In addition, we found that under some circumstances there was a frequency-dependent equilibrium in which both strategies can coexist in nature and we investigated whether signs of the presence of these two strategies could be found in a natural population.

Importantly, the analysis of real data coming from experiments on *L. hispanica* (Rabaneda-Bueno et al. 2008; 2014) showed that these two strategies can be present (coexist) in a wild population, as according to what we predicted we found 1) a negative correlation between the time of maturation and an estimate of voracity (the rate of weight gain – Rabaneda-Bueno et al. 2014), and that 2) the females that gained weight before mating (i.e., they were actively foraging) matured 20 days earlier than the females that lost weight (very close to the 17 days difference between the simulated strategies). Additionally, we found that the presumed MFCL females (i.e. those that had killed a male only after mating) used adaptive foraging plasticity, maturing later and waiting to mate with a male before attacking both prey or males and then immediately switching to become highly voracious towards both males and heterospecific prey.

Our sensitivity analysis of our simulations showed that the key advantage for the EARLY-SPOV strategy was having a low predation rate upon spillover juveniles (the parameter "different") and thus a low cost for boldness. Also, the high encounter rate between males and females for EARLY-SPOV females results in reduced male densities for the late-maturing MFCL females. Data on encounter rate of males and females and the rate of sexual cannibalism in sexually cannibalistic species support this idea. The crab spider *Misumena vatia* has a low rate of premating sexual cannibalism (<7.6%, Morse 2004) in accord with low male-female encounter frequencies (<1 female every two days--Morse 2007). Thus, for *M. vatia*,"maxenc"=0.5. But sexual size dimorphism is extreme in this species, with females being several times larger than males (Legrend and Morse 2000), perhaps making sexual cannibalism less desirable for females because the nutritional value of males could be too low. However, in fishing spiders of the genus *Dolomedes* (Arnqvist and Henriksson 1997; Johnson and Sih 2005, 2007) the encounter rate must be much higher. This is because females do not defend central territories, but raft around on ponds moving rapidly (Kreiter and Wise 1996). Also, higher encounter rates may be explained because females that reach maturity probably increase their foraging movements to meet the energy demands of egg production (Kreiter and Wise 2001). Since with few exceptions (Aisenberg et al. 2007) spider males are the searching sex and move around at a higher rate than females (Foellmer and Moya-Laraño 2007), the rate of encounter between the sexes must be very high, making the spillover strategy more viable in these spiders. As we gather more information on the natural rate of encounter between the sexes across sexually cannibalistic species, we will be better able to test the hypothesis that higher encounter rate leads to higher female aggression levels.

The aggression levels of spillover females need to be high for this strategy to be maintained in populations. The sensitivity analysis showed that reducing the probability for an EARLY-SPOV female to attack a male resulted in two new scenarios in which MFCL persisted. This makes sense, as low aggressive levels mean low male mortality and no shortage of males for MFCL females. However, our results also showed that behaving less aggressively towards males in poor environments can benefit EARLY-SPOV, likely because the shortness of prey affects more strongly to MFCL females.

The availability of alternative prey also helped determine which strategy prevailed, benefiting MFCL females only in one additional ecological scenario. Furthermore, when including Condition-Dependent SPOV or EARLY-SPOV females, in which what they fed as adults affected offspring production, produced results that were not qualitatively different from the basic scheme (see Arnqvist and Henricksson 1997). This result is counterintuitive, as sexual cannibalism may be a strategy to alleviate food limitation (Hurd et al. 1994; Moya-Laraño et al. 2003b; Rabaneda-Bueno et al. 2008) and adult foraging has been shown to greatly affect spider success (Moya-Laraño 2002; Rabaneda-Bueno et al. 2008) even in a fishing spider (Johnson and Sih 2005). Additional simulations including variation in the quality of the prey such as C:N content (since high N content may help account for pre-mating sexual cannibalism--Rabaneda-Bueno et al. 2008 and Rabaneda-Bueno, Mayntz and Moya-Laraño *unpublished data*) could help to solve this apparent paradox.

As expected, the costs associated with the spillover behavioral syndrome (i.e. juvenile and adult mortality from predation) had an important role in determining which strategy prevailed. Thus, a spillover behavioral syndrome is more likely to be maintained in populations that have relatively low predation pressure. In order to test the prediction that the spillover (or the early-maturing spillover) strategy is more likely in low-predation environments, the rates of predation upon juveniles and adults should be compared among populations and across species.

A potential drawback of our simulations is that the levels of aggression and boldness were determined by a single sex-linked gene, while behavioral syndromes are quantitative in nature. However, since we performed a detailed sensitivity analysis in which we plaid with different levels of correlation among behaviors and ecological constraints (e.g., probability of attacking males, foraging success, differences in mortality between strategies) we think that including a more complex quantitative genetic basis for our strategies (e.g. Moya-Laraño et al. 2012; 2014) would have resulted in qualitatively similar results.

Ecological determinants of the Frequency-Dependent equilibrium

Frequency-dependent selection can help explain the maintenance of polymorphisms in natural populations (Fisher 1930; Wright 1942; Clarke and O'Donald 1962). However, examples of this type of selection and evidence that it actually leads to the maintenance of polymorphisms are scant (e.g. Fitzpatrick et al. 2007). Recently, it has been suggested that negative frequency-dependent selection may be important in the maintenance of behavioral polymorphisms in populations (Wolf et al. 2007; Wolf & Weissing 2010). For example, in colonies of social spiders aggressive phenotypes are favorable under low frequencies but they tend to be sub-optimal when the proportion of aggressive individuals increase, which may be taken by non-aggressive individuals to outperform the aggressive type (Pruitt and Riechert, 2009b), This negative frequency-dependent mechanism can sustain mixtures of different behavioral phenotypes and would allow populations to evolve towards optima equilibrium in which different strategies have similar expected fitness functions (Maynard Smith 1982).

Therefore, understanding which ecological factors (selective pressures) may favor the evolution of these equilibria may be of central importance. A close study of the equilibrium shown in the results allowed us to identify the ecological mechanisms behind these equilibria (Electronic Appendix). First, male survival was low (more males died and in shorter time) at high frequencies of highly aggressive EARLY-SPOV females (TOP position in the equilibrium), as the earliest maturing females within the EARLY-SPOV strategy had more access to males than the latest maturing females. Since early-maturation meant smaller body size (following the equations in Table 1), the average mean fitness for EARLY-SPOV females decreased because smaller females have lower fecundity. Furthermore, MFCL females, by having a less-aggressive strategy, benefitted when males were scarce at high EARLY-SPOV frequencies. This allowed MFCL females to enjoy relatively higher mating success and thus higher fitness at the TOP position of the equilibrium. It is remarkable that the tiniest differences in fitness and mating success can produce a frequency-dependent equilibrium, suggesting that demonstrating in nature the causes of equilibria like this one may turn to be very challenging.

Arnqvist and Henriksson (1997) proposed that in natural populations, intermediate levels of aggression should be maintained. Our finding that frequency-dependent selection can maintain two alleles, one more aggressive than the other, supports this view. Our field data, however, suggests that the frequency of MFCL females (17 females that killed at least one male after the female had first mated) may be higher than that of EARLY-SPOV (7 females that killed at least one male before the female had first mated). The reasons behind these relative frequencies are difficult to know without further research. However, the fact that both strategies coexist is a relevant qualitative prediction of our model that has been met.

Behavioral syndromes and genotype-environment interactions in fitness

The existence of behavioral syndromes points to limits of adaptive behavioral plasticity, as correlation of behaviors across contexts implies that the most optimal behavior is not always displayed in all contexts (Sih et al. 2004a, b). The spillover strategy is one example of behavioral syndrome in which selection for high levels of aggression leading to fast growth in juveniles and large adult body sizes (and thus higher fecundity) may lead to a decrease in fitness in the mating context. This is especially true when males are a scarce resource and are killed by these highly aggressive females even when these females have not yet obtained sperm (Arnqvist and Henriksson 1997; Sih et al. 2004a, b; Johnson and Sih 2005, 2007). However, we show how female spiders may also evolve behavioral plasticity by lowering their foraging rate even to the point of losing weight and that this strategy (MFCL) may coexist with spillover individuals. Indeed, Neff and Sherman (2004) suggest that animals are probably able to be behaviorally plastic in many situations in which constraints can be neglected and use darwinian algorithms, by which the behavior that is most rewarding in terms of fitness would be displayed in each context. However, this is not to say that there are no limits to behavioral plasticity, as they surely are (e.g. Ruiz-Gómez et al. 2008; Brodin 2009; Minderman et al. 2009) and this may largely explain why behavioral syndromes have been documented in several occasions (e.g. Nelson et al. 2008; Logue et al. 2009; Wilson and Godin 2009).

Until now, researchers thought that in spiders, females could achieve behavioral plasticity in the context of sexual cannibalism through either 1) Distinguishing males from other potential prey or 2) decreasing general aggression levels until they mate at least once. If mate recognition is constrained and females cannot distinguish conspecific males from heterospecific prey (Gould 1984) then females can only be plastic by decreasing aggression levels against both males and prey. Decreasing the rate of attack upon heterospecific prey can be highly costly, because female spiders are often food limited (Wise 1993). Interestingly, in *Dolomedes triton* there is a time window of a few days during which recently matured females show very low levels of aggression, switching back to high aggression levels afterwards regardless of whether they have mated or not (Kreiter et al. *unpublished manuscript*), suggesting limitations in mate recognition and thus limits to plasticity. Here, we have reported how the presumed MFCL females in a wild population of *L. hispanica* are likely to decrease their voracity even to the point of losing weight. However, we also show how the great flexibility of this strategy allows these females to adaptively switch to a very high rate of food acquisition (both of males and heterospecific prey) once they have mated, like allowing to partially compensate their previous losses.

Concluding remarks

We have detected the ecological scenarios that can maintain, and determine the evolution of, a modified version of the spillover behavioral syndrome in which spillover females do not only grow to a larger size but also mature earlier. The main ecological determinants favoring this early-spillover strategy are low predation rates on both offspring and adults as well as a high encounter rate between males and females. However, in most ecological scenarios an alternative strategy in which females wait to have sperm to attack males or attack them only if food availability is low, seems to prevail. Consistently with the finding that the two strategies can coexist in frequency-dependent equilibrium, we found evidence that the two strategies are present in a population of the burrowing wolf spider *L. hispanica*. Our results increase our understanding of how behavioral syndromes can be maintained and even evolve in natural populations, as well as what determines the maintenance of behavioral types (personalities). We have also

detected the ecological scenarios that allow the coexistence of two rather extreme strategies via frequency-dependent selection, for which there are very few examples in nature.

Acknowledgements

We dedicate this paper to the memory of Nancy Kreiter. This study was initiated in a graduate course taught by PHC. Albert Torrents and Oriol Verdeny expanded Ungoliant ran parallel sensitivity analyses and provided helpful comments for this paper. Ungoliant is an insatiable spider in the Silmarillion of JRR Tolkien. We benefitted from helpful discussions associated with annual symposia of the Center for Ecology, Evolution and Behavior at UK. This work was partially financed by grant CGL2004-03153 to JML.

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ELECTRONIC APPENDIX

Sensitivity analysis

We ran a detailed series of simulations in order to disentangle which parameters parameter values were more important in determining the strategy more likely to prevail. We focused on the two most competitive strategies of interest (EARLY-SPOV *vs*. MFCL, and the procedure was as follows. We interchanged one of the parameters that differed between poor and rich environments at a time (i.e. we assigned the value originally in rich environments to poor environments and *vice versa*) and reran all the simulations in the basic scheme for maintenance (one run of the basic scheme for each of the interchanged parameters: prey availability, pspov, maxenc and mort; see Table 1). This allowed us to reveal what parameters were more important at determining which strategy was maintained in either rich or poor environments. Furthermore, we took these parameters for rich and poor environments and when possible, ran the basic simulation scheme by either multiplying each of the parameters (one parameter at a time for each run) by 3, or dividing it by 3.

We also contrasted the pure SPOV strategy against MFCL when SPOV females were –rather unrealistically- 44% as large as MFCL females and when adult feeding did not affect MFCL reproductive output. This was to see if at an extreme in differences in body sizes and with fecundity only affected by fixed adult body size, as assumed by Arnqvist and Henriksson (1997), the pure SPOV strategy could be maintained in natural populations.

Finally, because we found the parameter "maxenc" to be most responsible for which strategy persisted in poor or rich environments, we ran a last simulation in which we multiplied maxenc by 3 and started with pallele=0.01 for EARLY-SPOV against MFCL. This simulation was set to establish weather a very high probability of encounter between the sexes –which was found to be critical for EARLY-SPOV during sensitivity analysis- could widen the set of scenarios in which EARLY-SPOV can invade MFCL.

We also ran several other simulations with different parameter values, but since the results did not change our conclusions qualitatively, we do not mention the results here (see Table A1).

Results

Table A1 summarizes the results of the sensitivity analysis, which revealed that the parameter most responsible for the differences found in which strategy was maintained in either rich or poor environments was "maxenc", as we found that when this parameter was switched between environments, in one of the cases (different=0.7) the opposite strategy was maintained (Table A1 column R). Thus, in our simulations within the main text, EARLY-SPOV prevailed in rich environments because the probability of encounter is high. Another parameter that is important for the prevalence of EARLY-SPOV in rich environments is "pspov", as switching to lower probabilities of attack by EARLY-SPOV in a poor environment, this strategy was able to be maintained in one additional case (different=0.7 and recessive EARLY-SPOV, Table A1 column S). Prey availability also had an important effect for the prevalence of the MFCL strategy, as switching to high prey availability in an otherwise poor environment made MFCL to prevail in front of EARLY-SPOV (in the case for different=0.9 and recessive EARLY-SPOV, Table A1 column U). However, "maxenc" was a much important parameter, as higher prey availability was not enough in the basic scheme for MFCL to prevail when juvenile EARLY-SPOV survival was substantially high (different=0.7, 0.9 and recessive EARLY-SPOV; compare Table A1 columns R and U). Furthermore, mutiplying "maxenc" by 3 resulted in EARLY-SPOV persisting in populations in 3 new combinations of parameters and also added one new frequency-dependent equilibrium and another quasi-equilibrium (Table A1 column Q). The higher mortality of EARLY-SPOV females (parameter "mort") had no effect between environments, as switching this parameter did not change any qualitative result (Table A1 column T). However, multiplying the differential mortality of adult females ("mort") by 3 (i.e., 0.0030*4.5 to determine the mortality rate of SPOV females), did result in two new scenarios in which MFCL females persisted in populations in front of EARLY-SPOV (different=0.9 in poor environments and different=0.5 in rich enviroments,

Table A1 column W). Dividing "mort" by 3 did not provide qualitatively different results than the basic scheme of Fig. 2 (Table A1 column V). Multiplying prey availability by 3 also resulted in MFCL persisting in the same two additional scenarios as when increasing the relative mortality of EARLY-SPOV females (different=0.9 in poor environments and different=0.5 in rich enviroments, Table A1 column X). However, dividing prey by 3 had no qualitative effects (Table A1 column Y). Dividing the probability of EARLY-SPOV attack upon an approaching male ("pspov") by 3 resulted in MFCL prevailing in two additional scenarios in front of EARLY-SPOV (different=0.5, 0.7 in rich environments and recessive EARLY-SPOV, Table A1 column AB).

When we simulated very large pure SPOV females, we found that in rich environments and with very high survival of juvenile SPOV (different=0.9), the SPOV strategy could be maintained either in a frequency-dependent equilibrium with MFCL (dominant SPOV) or even alone (recessive SPOV, Table A1 column M).

When the male-female encounter rate was multiplied by 3, we found that a mutation of dominant EARLY-SPOV arising in a pure population of MFCL (i.e., starting frequency of SPOV allele of 0.01), could invade the population in two additional scenarios as compared with the scheme investigating the evolution of strategies in Fig. 4, one in which the MFCL strategy went extinct (different=0.9 in rich environments) and another in which both strategies were maintained in a frequency-dependent equilibrium (different=0.7 in rich environments, Table A1 column AK). Thus, encounter rates between males and females can also affect the evolution of strategies, even leading to coexistence (see also Table A1 column AJ for an unrealistic encounter rate).

Table 1. List of parameters as calculated from studies in *L. hispanica* (sources: Moya-Laraño 1999; Moya-Laraño 2002; Moya-Laraño 2003a,b; Moya-Laraño et al. 2004; J. Moya-Laraño *unpublished*)

Date of season's onset	April 23rd
Season length	79 days
Background female mortality rate for MFCL,	0.0030 day^{-1}
Background female mortality rate for SPOV, CD-SPOV, EM-SPOV and CD EM-SPOV *	0.0036 day^{-1}
Background male mortality rate	0.0045 day^{-1}
Female maturation time, "fem_mat" (since April 23rd) for MFCL	N|μ=56, σ=0.5|
Female maturation time, "fem_mat2 (since April 23rd) for EM-SPOV, and CD-SPOV and CD E SPOV	N|μ=39, σ=0.5|
Male maturation time, "mal_mat" (since April 23rd)	N|μ=36, σ=0.5|
Adult body size, CW (mm) for EM-SPOV and CD EM-SPOV	N|μ=3.21 + 0.047*fem_mat+ 0.39*CL, σ=0.4647|
Adult body size, CW (mm) for MFCL, SPOV and CD-SPOV	N|μ=3.21 + 0.024*fem_mat+ 0.39*CL, σ=0.4647|
Initial condition, $COND_o$ (mm)	N|μ=3.54 + 0.49*CW, σ=0.4576|
Threshold equation for female satiation (mm) **	-38.98+11.73*CW-0.63*CW^2
Added value on condition from feeding on a male	2.39 mm (~0.199 g)
Egg sac volume, vol (mm^3) for SPOV and EM-SPOV	N|μ=-1156.43+277.21*CW, σ=311.18|
Egg sac volume, vol (mm^3) for CD SPOV and CD EM-SPOV	N|μ=-1156.43+277.21*CW+123.44*$COND_f$, σ=311.18|
Egg sac volume, vol (mm^3) for MFCL	N|μ=-2297.64+217.88*CW+123.44*$COND_f$, σ=263.35|
Offspring number (N)	57.54 + 0.16*vol
Daily increase in condition (or daily net food balance in mm/day) for MFCL	U|0,1|*0.1482 ***
Daily increase in condition (or daily net food balance in mm/day) for SPOV, CD-SPOV, EM-SPOV and CD EM-SPOV	1.5*U|0,1|*0.1482 ***
Maximum daily rate of encounter with females, "maxenc"	1, 3 day^{-1}
Probability of an SPOV female attacking a male, "pspov"	0.5, 0.9
Probability of male escaping from a female attack, "pescape"	exp(-CW*0.1)
Offspring survival to maturation in SPOV, CD-SPOV, EM-SPOV and CD EM-SPOV, "different"	0.1, 0.3, 0.5, 0.7, 0.9

**In poor environments 0036 is replaced by 0.0045 (i.e. the parameter "mort"takes values 1.2 or 1.5 see Electronic Appendix).*

***Females with condition (mm) above this threshold do not feed anymore, attack males only if SPOV and are ready to lay an egg sac.*

****In poor environments 0.1482 is replaced by 0.0741.*

TABLE A1 – Sensitivity analysis showing which strategies prevail after 20,000 generations of simulation

PARAMETERS TO INITIALIZE SIMULATIONS (SPOV vs. MFCL)

filename	d	pspov	mort	different	prey	maxenc	BASIC SCHEME: EM-SPOV vs MFCL	PS vs. MFCL	PS vs. CW-MFCL	LARGE PS vs. CW-MFCL	PS (low pspov) vs. CW-MFCL
sim1a	1	0.9	1.5	0.1	low	1	MFCL	MFCL	MFCL	MFCL	MFCL
sim2a	1	0.9	1.5	0.3	low	1	MFCL	MFCL	MFCL	MFCL	MFCL
sim3a	**1**	**0.9**	**1.5**	**0.7**	**low**	**1**	EQUILIBRIUM (0.72)	MFCL	MFCL	MFCL	MFCL
sim4a	1	0.9	1.5	0.9	low	1	SPOV	MFCL	MFCL	MFCL	MFCL
sim5a	1	0.5	1.2	0.1	high	3	MFCL	MFCL	MFCL	MFCL	MFCL
sim6a	1	0.5	1.2	0.3	high	3	MFCL	MFCL	MFCL	MFCL	MFCL
sim7a	**1**	**0.5**	**1.2**	**0.7**	**high**	**3**	EQUILIBRIUM (0.81)	MFCL	MFCL	MFCL	MFCL
sim8a	**1**	**0.5**	**1.2**	**0.9**	**high**	**3**	QUASI-EQUILIBRIUM (17,860)	MFCL	MFCL	EQUILIBRIUM (0.512)	MFCL
sim9a	1	0.9	1.5	0.5	low	1	MFCL	MFCL	MFCL	MFCL	MFCL
sim10a	**1**	**0.5**	**1.2**	**0.5**	**high**	**3**	EQUILIBRIUM (0.54)	MFCL	MFCL	MFCL	MFCL
sim1b	2	0.9	1.5	0.1	low	1	MFCL	MFCL	MFCL	MFCL	MFCL
sim2b	2	0.9	1.5	0.3	low	1	MFCL	MFCL	MFCL	MFCL	MFCL
sim3b	2	**0.9**	**1.5**	**0.7**	**low**	**1**	MFCL	MFCL	MFCL	MFCL	MFCL
sim4b	2	0.9	1.5	0.9	low	1	SPOV	MFCL	MFCL	MFCL	MFCL
sim5b	2	0.5	1.2	0.1	high	3	MFCL	MFCL	MFCL	MFCL	MFCL
sim6b	2	0.5	1.2	0.3	high	3	MFCL	MFCL	MFCL	MFCL	MFCL
sim7b	2	**0.5**	**1.2**	**0.7**	**high**	**3**	SPOV	MFCL	MFCL	MFCL	MFCL
sim8b	2	**0.5**	**1.2**	**0.9**	**high**	**3**	SPOV	MFCL	MFCL	SPOV	MFCL
sim9b	2	0.9	1.5	0.5	low	1	MFCL	MFCL	MFCL	MFCL	MFCL
sim10b	2	**0.5**	**1.2**	**0.5**	**high**	**3**	SPOV	MFCL	MFCL	MFCL	MFCL

RICH ENVIRONMENT
POOR ENVIRONMENT

Same color indicate opposite WINNING strategies in rich vs poor environments

d – dominance, 1-SPOV DOMINANT, 2-MFCL DOMINANT
pspov – probability for the female of attacking and approaching males
mort – multiplies the MFCL adult female mortality (0.003 per day) to determine SPOV mortality
different – proportion of born SPOV that reach maturation
prey – prey availability (estimated in mm/day of abdomen growth; high=0.1482, low=0.0741)
maxenc – maximum number of females encountered per male in one day

STRATEGY ABBREVIATIONS

EM-SPOV: Early-Maturing Spillover Strategy
PS: Pure Spillover Strategy (maturing times are identical to MFCL)
MFCL: Mate First and Cannibalize Later Strategy
CW-MFCL: Mate First and Cannibalize Later Strategy but in which fecundity in MFCL females depends only on the size of the carapace (not on adult feeding) *ADULT-COND-EM-SPOV:* Early-Maturing Spillover Strategy in which adult feeding also contributes to female fecundity

TABLE A1 (cont.'d)

	O	P	Q	R	S	T	U
1							
2	ADULT-COND-EM-SPOV vs. MFCL	ADULT-COND-PS vs. MFCL	MAXENC X 3 (*)	SWAP_MAXENC (*)	SWAP_pspov (*)	SWAP_MORT (*)	SWAP_PREY (*)
4	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
5	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
6	EQUILIBRIUM (0.75)	MFCL	EQUILIBRIUM (0.73)	QUASI-EQUILIBRIUM (8,811)	EQUILIBRIUM (0.76)	EQUILIBRIUM (0.82)	EQUILIBRIUM (0.78)
7	SPOV	MFCL	SPOV	SPOV	QUASI-EQUILIBRIUM (15,487)	SPOV	SPOV
8	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
9	MFCL	MFCL	QUASI-EQUILIBRIUM (5,246)	MFCL	MFCL	MFCL	MFCL
10	EQUILIBRIUM (0.80)	MFCL	EQUILIBRIUM (0.80)	EQUILIBRIUM (0.75)	QUASI-EQUILIBRIUM (12,291)	EQUILIBRIUM (0.78)	EQUILIBRIUM (0.79)
11	QUASI-EQUILIBRIUM (11,688)	MFCL	QUASI-EQUILIBRIUM (6,569)	EQUILIBRIUM (0.97)	SPOV	QUASI-EQUILIBRIUM (3,764)	QUASI-EQUILIBRIUM (2,166
12	MFCL	MFCL	EQUILIBRIUM (0.59)	EQUILIBRIUM (0.54)	MFCL	MFCL	MFCL
13	EQUILIBRIUM (0.543)	MFCL	EQUILIBRIUM (0.57)	MFCL	EQUILIBRIUM (0.52)	EQUILIBRIUM (0.56)	EQUILIBRIUM (0.57)
15	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
16	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
17	MFCL	MFCL	SPOV	SPOV	SPOV	MFCL	MFCL
18	SPOV	MFCL	SPOV	SPOV	SPOV	SPOV	MFCL
19	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
20	MFCL	MFCL	SPOV	MFCL	MFCL	MFCL	MFCL
21	SPOV	MFCL	SPOV	MFCL	SPOV	SPOV	SPOV
22	SPOV	MFCL	SPOV	SPOV	SPOV	SPOV	SPOV
23	MFCL	MFCL	SPOV	SPOV	MFCL	MFCL	MFCL
24	SPOV	MFCL	SPOV	MFCL	SPOV	SPOV	SPOV
25							

(*) Indicates changing this parameter relative to the basic scheme in column J (SWAP means changing the target parameter between rich and poor environments)

TABLE A1 (cont.'d)

	V	W	X	Y	Z	AA	AB
1							
2	MORT_0.5 (*)	MORT_4.5 (*)	PREY_X_3 (*)	PREY_X_0.33 (*)	PSALLEL_0.01 (**)	PSALLEL_0.99 (**)	PSPOV_X_0.33 (**)
3							
4	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
5	MFCL	MFCL	MFCL	MFCL	MFCL	SPOV	MFCL
6	EQUILIBRIUM (0.85)	MFCL	EQUILIBRIUM (0.72)	QUASI-EQUILIBRIUM (7,931)	MFCL	SPOV	MFCL
7	SPOV	SPOV	SPOV	SPOV	MFCL	SPOV	EQUILIBRIUM (0.92)
8	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
9	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
10	EQUILIBRIUM (0.79)	EQUILIBRIUM (0.8)	EQUILIBRIUM (0.78)	EQUILIBRIUM (0.79)	MFCL	EQUILIBRIUM (0.8)	EQUILIBRIUM (0.63)
11	QUASI-EQUILIBRIUM (11,242)	QUASI-EQUILIBRIUM (1,225)	QUASI-EQUILIBRIUM (10,413)	QUASI-EQUILIBRIUM (1,064)	QUASI-EQUILIBRIUM (1,913)	QUASI-EQUILIBRIUM (10,266)	EQUILIBRIUM (0.92)
12	MFCL	MFCL	MFCL	MFCL	MFCL	SPOV	MFCL
13	EQUILIBRIUM (0.57)	EQUILIBRIUM (0.54)	EQUILIBRIUM (0.57)	EQUILIBRIUM (0.56)	MFCL	EQUILIBRIUM (0.57)	MFCL
14							
15	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
16	MFCL	MFCL	MFCL	MFCL	MFCL	SPOV	MFCL
17	MFCL	MFCL	MFCL	MFCL	MFCL	SPOV	MFCL
18	SPOV	MFCL	MFCL	SPOV	MFCL	SPOV	SPOV
19	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
20	MFCL	MFCL	MFCL	MFCL	MFCL	SPOV	MFCL
21	SPOV	SPOV	SPOV	SPOV	MFCL	SPOV	MFCL
22	SPOV	SPOV	SPOV	SPOV	MFCL	SPOV	SPOV
23	MFCL	MFCL	MFCL	MFCL	MFCL	SPOV	MFCL
24	SPOV	MFCL	MFCL	SPOV	MFCL	SPOV	MFCL
25							

(**) PSALLEL is the frequency of the allel for the EM-SPOV strategy

TABLE A1 (cont.'d)

	AC	AD	AE	AF	AG	AH	AI
1							
2	SEXDIFMORT_X3	EM-SPOV vs. CW-MFCL	SWAP_MORT_4.5_vs_1.2	SEX_DIF_MORT_X200	SEX_DIF_MORT_X20	PS vs. CW-MFCL MAXENC X3	PSALLEL_0.99 PREY X 3
3							
4	MFCL	MFCL		MFCL	MFCL	MFCL	MFCL
5	MFCL	MFCL		MFCL	MFCL	MFCL	MFCL
6	EQUILIBRIUM (0.74)	EQUILIBRIUM (0.71)		SPOV	EQUILIBRIUM	MFCL	SPOV
7	SPOV	SPOV		SPOV	SPOV	MFCL	SPOV
8	MFCL	MFCL		MFCL	MFCL	MFCL	MFCL
9	MFCL	MFCL		EQUILIBRIUM <0.5!!	MFCL	MFCL	MFCL
10	EQUILIBRIUM (0.80)	EQUILIBRIUM (0.80)		EQUILIBRIUM	EQUILIBRIUM	MFCL	EQUILIBRIUM
11	EQUILIBRIUM	QUASI-EQUILIBRIUM (5,466)		QUASI-EQUILIBRIUM	QUASI-EQUILIBRIUM	MFCL	EQUILIBRIUM
12	MFCL	MFCL		EQUILIBRIUM	MFCL	MFCL	SPOV
13	EQUILIBRIUM (0.57)	EQUILIBRIUM (0.58)		EQUILIBRIUM	EQUILIBRIUM	MFCL	EQUILIBRIUM
14							
15	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
16	MFCL	MFCL	MFCL	SPOV	MFCL	MFCL	SPOV
17	MFCL	MFCL	MFCL	SPOV	MFCL	MFCL	SPOV
18	SPOV	MFCL	SPOV	SPOV	SPOV	MFCL	SPOV
19	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL	MFCL
20	MFCL	MFCL	MFCL	SPOV	MFCL	MFCL	SPOV
21	SPOV	SPOV	MFCL	SPOV	MFCL	MFCL	SPOV
22	SPOV	SPOV	SPOV	SPOV	SPOV	MFCL	SPOV
23	MFCL	MFCL	MFCL	SPOV	MFCL	MFCL	SPOV
24	SPOV	SPOV	SPOV	SPOV	SPOV	MFCL	SPOV
25							

TABLE A1 (cont.'d)

	AJ	AK	AL	AM	AN
1					
2	PSALLEL_0.01 MAXENC X 50	PSALLEL_0.01 MAXENC X 3	PSALLEL_0.01 DEV TIME SPOV 48	PSALLEL_0.01 DEV TIME SPOV 52	PSALLEL_0.01 DEV TIME SPOV 52 EQ. SLOPES
3					
4	MFCL	MFCL	MFCL	MFCL	
5	MFCL	MFCL	MFCL	MFCL	
6	QUASI-EQUILIBRIUM (19,024)	MFCL	MFCL	MFCL	
7	SPOV	SPOV	MFCL	MFCL	
8	MFCL	MFCL	MFCL	MFCL	
9	EQUILIBRIUM < 0.5!!	MFCL	MFCL	MFCL	
10	EQUILIBRIUM	EQUILIBRIUM	MFCL	MFCL	
11	SPOV	QUASI-EQUILIBRIUM (1,774)	QUASI-EQUILIBRIUM (1,867)	EQUILIBRIUM (0.90)	MFCL
12	EQUILIBRIUM	MFCL	MFCL	MFCL	
13	EQUILIBRIUM	MFCL	MFCL	MFCL	
14					
15	MFCL	MFCL	MFCL	MFCL	
16	MFCL	MFCL	MFCL	MFCL	
17	MFCL	MFCL	MFCL	MFCL	
18	MFCL	MFCL	MFCL	MFCL	
19	MFCL	MFCL	MFCL	MFCL	
20	MFCL	MFCL	MFCL	MFCL	
21	MFCL	MFCL	MFCL	MFCL	
22	MFCL	MFCL	MFCL	MFCL	
23	MFCL	MFCL	MFCL	MFCL	
24	MFCL	MFCL	MFCL	MFCL	
25					

TABLE A1 (cont.'d)

	AO	AP	AQ	AR
1				
2	PSALLEL_0.01 DEV TIME SPOV 52 SLOP SPOV 0.28	PSALLEL_0.01 DEV TIME SPOV 52 SLOP SPOV 0.34	MORT_4.5_vs_1.2	EARLY MATURING SPOV DEV TIME 48
4				MFCL
5				MFCL
6				MFCL
7				MFCL
8				MFCL
9				MFCL
10				EQUILIBRIUM (0.69)
11	MFCL	EQUILIBRIUM (0.78)		QUASI-EQUILIBRIUM (1,908)
12				MFCL
13				MFCL
15			MFCL	MFCL
16			MFCL	MFCL
17			MFCL	MFCL
18			MFCL	MFCL
19			MFCL	MFCL
20			MFCL	MFCL
21			SPOV	SPOV
22			SPOV	SPOV
23			MFCL	MFCL
24			SPOV	MFCL
25				

TABLE A1 (cont.'d)

	AS	AT	AU	AV
1				
2	EARLY MATURING SPOV SLOP 0.036	EARLY MATURING SPOV DEV TIME 52	EARLY MATURING SPOV SLOP 0.030	EARLY MATURING SPOV SLOP 0.027
3				
4	MFCL	MFCL	MFCL	
5	MFCL	MFCL	MFCL	
6	EQUILIBRIUM (0.73)	MFCL	EQUILIBRIUM (0.72)	
7	SPOV	MFCL	SPOV	
8	MFCL	MFCL	MFCL	
9	MFCL	MFCL	MFCL	
10	EQUILIBRIUM (0.78)	MFCL	EQUILIBRIUM (0.79)	
11	QUASI-EQUILIBRIUM (1,443)	EQUILIBRIUM (0.91)	QUASI-EQUILIBRIUM (5,297)	
12	MFCL	MFCL	MFCL	
13	EQUILIBRIUM (0.55)	MFCL	EQUILIBRIUM (0.54)	
14				
15	MFCL	MFCL	MFCL	
16	MFCL	MFCL	MFCL	
17	MFCL	MFCL	MFCL	
18	SPOV	MFCL	SPOV	MFCL
19	MFCL	MFCL	MFCL	
20	MFCL	MFCL	MFCL	
21	SPOV	MFCL	SPOV	
22	SPOV	SPOV	SPOV	
23	MFCL	MFCL	MFCL	
24	SPOV	MFCL	MFCL	MFCL
25				

DISCUSIÓN GENERAL INTEGRADORA

Discusión

Los resultados del manuscrito I de esta tesis ponen de manifiesto que el canibalismo sexual pre-cópula es un comportamiento frecuente en poblaciones naturales de la tarántula ibérica (*Lycosa hispanica*), ya que 1/3 de las hembras en el experimento de campo 1 atacó y consumió un macho. En la inmensa mayoría de los casos las hembras caníbales no se habían apareado previamente con el macho que habían canibalizado (canibalismo sexual pre-cópula), pero sí con otro diferente. En el presente estudio, la disponibilidad local de machos entra dentro del intervalo natural de la especie, y refleja una variación natural en la tasa de visitas a lo largo de la estación reproductora. Estos resultados podrían ser útiles para explicar los efectos de la densidad poblacional en las tasas de canibalismo, que han sido relativamente poco estudiados (Hebets, 2003, Johnson, 2005) y nunca se habían estudiado hasta la fecha en el campo.

La densidad poblacional de *L. hispanica* puede disminuir a lo largo de la temporada como consecuencia de la depredación (escorpiones, zorros, jabalíes, aves), y puede provocar cambios en la proporción de sexos ("sex ratio") poblacional en favor de las hembras debido al canibalismo sexual (Moya-Laraño et al., 2003a,c). Sin embargo, estas variaciones en la proporción de sexos poblacional debidas al canibalismo y la depredación no son los únicos factores determinantes de la disponibilidad local de machos para las hembras. El comportamiento de los machos también puede ser importante, ya que su movilidad durante la búsqueda activa de pareja es variable (De Mas et al. 2009; Corcobado, 2011). Por su parte, las hembras deberían responder a la variación en la densidad local de machos, ya que podría ser la única estima disponible para evaluar qué cantidad de machos tienen a su disposición. Partiendo de las frecuencias de canibalismo sexual observadas en este estudio, dos resultados obtenidos en los experimentos 1 y 2 (manuscrito I) sugieren que el canibalismo sexual pre-cópula es un comportamiento adaptativo, que varía dependiendo de la disponibilidad de machos como fuente de esperma y alimento, lo que es consistente con la hipótesis del forrajeo adaptativo (Newman & Elgar, 1991). En primer lugar, la mayoría de las hembras que atacaron y

consumieron un macho (92% en el primer experimento y 91% en el segundo experimento) no eran vírgenes y, por tanto, disponían de esperma para fertilizar sus huevos. Por el contrario, la proporción de hembras vírgenes que atacó un macho fue muy baja (8% en el primer experimento y 9% en el segundo experimento). La tasa de ataques aumentó considerablemente una vez que las hembras se hubieron apareado, y un 25% de las hembras atacaron machos después de haber copulado (experimento 1), un patrón similar al observado en otras especies (Johnson, 2001; Elgar, 1998; Herberstein et al., 2002; Erez et al., 2005). En segundo lugar, la tasa de canibalismo sexual aumentó con la densidad de machos e independientemente de la tasa de encuentros macho-hembra, sugiriendo que antes de atacar, las hembras evaluaron la disponibilidad de machos en el ambiente. Un estudio en la araña pescadora (*Dolomedes triton*) apoya esta idea, ya que indirectamente sugiere que las hembras pueden valorar si el ambiente es pobre o rico en machos (Johnson, 2005).

Los resultados del experimento 2 (manuscrito I) ponen de manifiesto que los machos son presas cualitativamente relevantes para la dieta de las hembras, con importantes efectos positivos sobre la eficacia biológica de éstas. Entre los beneficios de fecundidad del canibalismo (experimento 2, 3, manuscrito I) se incluyen un mayor número de crías, crías de mejor condición corporal o una puesta más temprana, que implica el nacimiento anticipado de las arañitas y una ventaja competitiva de tamaño sobre las crías de madres no caníbales (de dispersión tardía). Este último resultado es consistente con los patrones de depredación y canibalismo intragremial observados en otras especies de arañas lobo, en las que los individuos más grandes depredan sobre los más pequeños (Samu et al., 1999; Buddle et al., 2003). Por otra parte, muy pocos estudios han demostrado que el consumo de un macho sea beneficioso para la fecundidad de las hembras, y las escasas evidencias pertenecen a especies con pocas diferencias de tamaño entre los sexos (Ej: Berning et al., 2012). Los machos de *L. hispanica* tienen un tamaño mucho mayor que las presas naturales de esta araña, que incluyen sobre todo isópodos y escarabajos tenebriónidos (Moya-Laraño et al., 2002), y su contenido calórico debería ser relativamente alto, aunque el aporte de calorías puede no ser la única ventaja que proporcionen los machos. Un resultado del experimento 2 (manuscrito I) sugiere que los machos podrían ser un importante

suministro de nitrógeno (proteína), ya que las hembras que consumieron un macho tenían mayor probabilidad de cerrar su nido con seda que las hembras que no lo consumieron. La producción de seda para cerrar el nido puede ser un rasgo conductual potencialmente seleccionable, ya que tendría efectos positivos sobre la eficacia biológica de las hembras al reducir el riesgo de depredación de la puesta durante la fase de desarrollo. Sin embargo, debido a su alto contenido en nitrógeno, la producción de seda es nutricionalmente costosa (Craig, 2003), y la calidad de ésta va a depender en gran parte de la calidad de la dieta (Craig et al., 2000). Los machos de *L. hispanica* son artrópodos depredadores con un contenido en nitrógeno superior al de sus presas detritívoras (J. Moya-Laraño, R. Rabaneda-Bueno y D. Mayntz, datos no publicados), por lo que el consumo de proteínas provenientes del macho serviría para contrarrestar la limitación de nitrógeno, que se ha sugerido existe en poblaciones naturales (Moya-Laraño et al., 2008), y permitiría a las hembras afrontar mejor los costes de producir seda (Craig et al., 2000; Mayntz et al., 2005; Blamires & Tso, 2013). Los machos constituirían por tanto un suministro importante de nitrógeno para las hembras, cuya composición nutricional puede estar directamente relacionada con el contenido nutricional de las presas en su dieta (Hawley et al., 2014). En algunas especies de arañas lobo (Lycosidae), la depredación sobre conespecificos supone una mejora sustancial en la eficiencia de forrajeo de la araña con respecto al consumo de presas naturales (Mayntz & Toft, 2006), cuya carencia de determinados nutrientes puede llevar a una limitación enzimática y nutricional incluso si hay abundantes recursos alimenticios (Samu, 1993). Por ejemplo, los machos de algunas arañas pueden contener aminoácidos esenciales en proporciones similares a las requeridas por las hembras que no tienen sus presas naturales (Denno & Fagan, 2003). Por último, sería interesante investigar si existen diferencias entre las hembras caníbales y no caníbales en el grado de elaboración de la decoración de sus nidos (brocal), ya que ésta tiene una función anti-depredadora en *L. hispanica* (Williams et al., 2006), y en otras especies se ha visto que las arañas con mayor ingesta de proteínas desarrollan elementos decorativos más prominentes (Blamires et al., 2009; Blamires & Tso, 2013), de modo que las hembras caníbales podrían disponer de defensas adicionales al tapón de seda tanto antes como durante la fase de maduración de la puesta.

Todo lo anterior sugiere que los machos, además de constituir una fuente inmediata de calorías, pueden ser un aporte importante de nitrógeno y de otros aminoácidos esenciales, que son difíciles de extraer o están ausentes en una dieta consistente únicamente en presas naturales. Los artrópodos depredadores tales como las arañas pueden no disponer de un mecanismo de regulación apropiado de su composición corporal porque la limitación de alimento (Wise, 1993) puede promover la ingesta y asimilación oportunista de nutrientes, lo que impediría ajustar la proporción de lípidos y proteínas que extraen de sus presas de acuerdo con la limitación y/o necesidades que tengan de estos nutrientes (Mayntz et al., 2005). En *L. hispanica*, el canibalismo podría contribuir a solventar los desequilibrios nutricionales de una dieta limitada, que el consumo activo de presas no puede cubrir y serviría para mejorar el procesamiento de nutrientes procedentes de otras presas, lo que puede ser especialmente relevante durante la fase de maduración del huevo. En esta araña, las hembras adultas parecen compensar la limitación por alimento (hambre) que experimentan durante la fase juvenil canibalizando machos (Moya-Laraño et al., 2003c), y en otras especies las hembras atacan a los machos en función de su nivel de hambre (Herberstein et al., 2002; Wilder & Rypstra, 2008; Berning et al., 2012). Dado que los artrópodos depredadores pueden cazar presas selectivamente, según sus necesidades nutricionales (Greenstone, 1979; Mayntz et al., 2005), sería interesante evaluar si la tendencia de las hembras a atacar machos varía en función de los desequilibrios nutricionales en su dieta a base de presas naturales.

Todos estos resultados son consistentes con la hipótesis del forrajeo adaptativo, e indican que en *L. hispanica* el canibalismo sexual pre-cópula pudo haber evolucionado como una estrategia de la hembra para paliar la limitación nutricional incrementando su eficacia biológica (Elgar & Nash, 1988; Newman & Elgar, 1991; Andrade, 1998). Más que representar un comportamiento de forrajeo oportunista, el canibalismo implicaría un forrajeo selectivo, ya que en este estudio todas las hembras disponían de una proporción de alimento similar y muy próxima a la de la naturaleza (en número de presas) y, sin embargo, las hembras que no consumieron un macho tuvieron peores registros de fecundidad que las hembras caníbales, sugiriendo que la limitación es en la calidad de las presas. Además, debido a que la mitad de las hembras recibió un macho que podía matar pero no

consumir y la otra mitad recibió un macho que sí pudo consumir, los beneficios de fecundidad de las hembras caníbales no son atribuibles al hecho de que éstas fueran más agresivas y, por tanto, más voraces cazando presas. Con esto puede descartarse que fuese la correlación genética entre el comportamiento caníbal y el de forrajeo la que explicara la mejora de fecundidad en el experimento.

Los resultados de los experimentos 1 y 2 (manuscritos I y II) son también consistentes con la hipótesis de la personalidad por salpicadura agresiva ("spillover") (Arnqvist & Henriksson, 1997). La primera evidencia es que algunas hembras vírgenes del tratamiento de baja densidad de machos tuvieron una alta tasa de ataques a machos, y como resultado no llegaron a copular y producir un saco de huevos al final de la estación reproductora. Las hembras demasiado agresivas tienen por tanto un alto riesgo de falta de fecundación, especialmente cuando la disponibilidad de machos es baja, una situación que podría ser frecuente en poblaciones naturales a medida que avanza la estación reproductora (Moya-Laraño et al., 2003a). Estos datos además indican la importancia de evaluar la abundancia natural de machos y/o la limitación espermática para poder entender los efectos del canibalismo sexual pre-cópula en el éxito reproductor de las hembras.

La segunda evidencia consistente con la hipótesis "spillover" es que la voracidad de forrajeo de las hembras, estimada a partir de las tasas de engorde, estuvo correlacionada con la probabilidad de que una hembra atacara un macho y, por tanto, con su tendencia al canibalismo sexual (manuscrito II). Las tasas de engorde y canibalismo fueron variables, indicando que las hembras expresan distintos niveles de agresividad hacia las presas (voracidad de forrajeo) y los machos (canibalismo sexual). Así, las hembras más voraces y con mayores tasas de ingesta de presas tienden a canibalizar machos indiscriminadamente antes de haber conseguido esperma, mientras que las hembras dóciles que son menos voraces alimentándose y tienen tasas de engorde más bajas antes de copular por primera vez tienden a copular más probablemente con los machos, aunque son selectivas y copulan con machos en mejor condición. Resulta interesante que los rasgos morfológicos y fisiológicos de la hembra, como el tamaño o la condición corporal, no afectaran a la probabilidad de cópula o de canibalismo, lo que pone de

manifiesto que la personalidad agresiva de la hembra, definida en el contexto de este estudio como la voracidad de forrajeo latente durante la estación reproductora, fue el único factor que predijo si una hembra atacaría un macho.

Además de la voracidad de forrajeo hay otros factores que pudieron contribuir a la variabilidad observada en las tasas de engorde de las hembras, tales como la variabilidad ambiental (cantidad y calidad de presas, exposición a depredadores y factores abióticos) y la eficiencia de asimilación. Sin embargo, en este estudio se pueden descartar estos factores como posibles causas de variabilidad por varias razones. En primer lugar, todas las hembras fueron aisladas en cercados individuales, cerrados por encima y muy próximos entre sí, con lo que se eliminó cualquier fuente potencial de depredación. Además, las hembras fueron alimentadas con una abundancia y composición de presas naturales aleatorizada entre individuos y por tanto muy similar entre ellos y a lo largo de la temporada reproductora ("jardín común"). Estos dos argumentos indican que la variabilidad ambiental entre las hembras fue prácticamente nula. En segundo lugar, entre las hembras pudo haber diferencias en la eficiencia de asimilación de alimento que generasen variabilidad en las tasas de engorde, de modo que algunas hembras, independientemente de su nivel de voracidad, procesaran mejor las presas capturadas que otras hembras. Aunque no se tienen datos de la eficiencia de asimilación en *L. hispanica*, en un taxón no muy lejano, *Lycosa godeffroyi* la eficiencia de asimilación es poco variable (dentro de ambientes CV=2-10%; entre ambientes, CV=5%) (Humphreys, 1977), y debido a que ambas especies son ecológicamente muy similares, podría asumirse que en *L. hispanica* la eficiencia de asimilación es también relativamente poco variable. Además, esto contrasta con que, en el presente estudio, la variabilidad en las tasas de engorde fue muy alta (CV = 189%), por lo que es muy probable que éstas reflejen simplemente diferencias en la voracidad alimentaria de las hembras. Por último, la variabilidad en las tasas de engorde podría ser el resultado de una combinación entre la eficiencia de asimilación y la variabilidad ambiental. Por ejemplo, en arañas lobo las tasas de engorde pueden disminuir cuando disminuye el contenido proteico de las presas (Mayntz & Toft, 2001), aunque las arañas en general son altamente resistentes a períodos prolongados de escasez de presas, a los que se aclimatan reduciendo su tasa metabólica (Wise, 1993; Foelix, 1996; Wang et al., 2006). Mediante el diseño

experimental utilizado en este estudio, se minimizaron estas posibles fuentes de variación interindividual, por lo que las diferencias en las tasas de engorde entre las hembras explicarían gran parte de la variación en voracidad. Por otro lado, la voracidad de forrajeo puede tener un componente agresivo (agresividad general) o ser una combinación de rasgos conductuales, que incluyen los niveles de actividad ("boldness" vs. "shyness" – individuos conspicuos contra individuos tímidos) y la habilidad de caza, los cuales pueden estar o no correlacionados entre sí (Moya-Laraño, 2002; Johnson & Sih, 2005) y tener una base genética (Riechert & Maynard-Smith, 1989; Riechert & Hedrick, 1993; Kralj-Fišer & Schneider, 2012). Sin embargo, se desconoce cómo interaccionan entre sí todos estos rasgos y cómo influirían en la variación en la agresividad y voracidad de las hembras. También se desconoce si estos rasgos son heredables en *L. hispanica,* aunque los resultados del experimento 2 (manuscritos I y III) apuntan en esta dirección, al sugerir efectos maternos y/o genéticos (familiares) en la variabilidad de crecimiento de las arañitas (ver también Uhl et al., 2004). De hecho, un estudio con otra especie de araña sugiere efectos de familia en la tendencia al canibalismo (Johnson et al., 2010).

Como adelantamos antes, el tamaño y/o la condición de la hembra no explican la tendencia al canibalismo (manuscrito II) y el tamaño fijo estructural tampoco influye en la fecundidad de la hembra (Moya-Laraño, 2002 y manuscrito I). De hecho los resultados del manuscrito I, junto a datos previos de *L. hispanica*, muestran que es la condición corporal, y no el tamaño, el determinante de la fecundidad de las hembras (Moya-Laraño, 2002). Además, estos resultados son inesperados por el hecho de que la correlación positiva entre voracidad alimenticia y canibalismo implica mayores tasas de ingesta de alimento, que deberían provocar un incremento en el tamaño y/o la condición de las hembras más agresivas (Moya-Laraño et al., 2003a,c), tal como predice la hipótesis "spillover" (Arnqvist & Henriksson, 1997).

Volviendo al manuscrito II, la clara distinción entre hembras agresivas y dóciles nos lleva a preguntarnos cuál de estos fenotipos conductuales es más costoso y cuál tiene una mayor probabilidad de desaparecer o mantenerse en la población. El manuscrito IV muestra que estos tipos conductuales se asocian a dos

estrategias diferentes en relación a los niveles de voracidad y canibalismo, que estarían genéticamente fijadas en la población. Por un lado, una estrategia agresiva de canibalismo indiscriminado (SPOV: "spillover"), y por otro, una estrategia más adaptativa de canibalismo dependiente de la condición del macho y del estado reproductor de la hembra (MFCL: "*Mate first and cannibalize later"*, en inglés). ¿Cuáles son los costes y los beneficios de cada estrategia?

Los resultados del manuscrito IV muestran que las hembras de *L. hispanica* de maduración temprana tienen mejor condición que las de maduración tardía. En línea con esta evidencia los modelos basados en los individuos (IBMs), junto con datos adicionales obtenidos del experimento 2, ponen de manifiesto que el momento de maduración y las tasas de engorde desempeñan un papel principal en el balance de costes y beneficios de las estrategias "SPOV" y "MFCL" (manuscrito IV). Quizás el hallazgo más sorprendente de esta tesis doctoral es que la coexistencia predicha de las dos estrategias se corrobora en los datos empíricos de una población de *L. hispanica*. Por un lado, las hembras "SPOV" que tienden a comerse a un macho antes de copular no cambian su alimentación y mantienen sus altos niveles de voracidad y tasa de ingesta de presas durante toda la estación reproductora. Por otro lado, las hembras más dóciles "MFCL", que primero copulan y después tienden a atacar machos, muestran un cambio significativo en su tasa de ingesta tras aparearse, que se acompaña de un cambio en su agresividad hacia los machos. Debido a que el efecto de una mayor voracidad alimentaria fue el acortamiento del tiempo de maduración, las hembras más agresivas "SPOV" maduraron antes, mientras que las hembras dóciles "MFCL" maduraron más tarde. Esto nos hace modificar la hipótesis SPOV y hablar de una estrategia EARLY-SPOV, en que madurar más tempranamente ofrece una ventaja muy superior a la que supone madurar a un tamaño superior con una mayor fecundidad. Por tanto, respondiendo a la pregunta anterior, el beneficio que obtienen las hembras "SPOV" por tener una mayor tasa de ingesta no es un mayor crecimiento, sino madurar antes, que es un factor clave para que esta estrategia sea favorecida respecto a una estrategia "MFCL". Curiosamente, los datos de campo muestran cómo las hembras de maduración temprana son más agresivas (mayor tasa de ingesta) y no cambian su comportamiento agresivo en toda la estación, mientras que las de maduración

tardía cambian tras la cópula a una alta tasa de ingesta (voracidad) que se correlaciona con una mayor tasa de ataque a los machos.

Adicionalmente, el cambio en la tasa de ganancia de peso antes y después de la cópula es crítico para entender los costes y beneficios de ambas estrategias. Así, las hembras "SPOV", más voraces y con mayores tasas de engorde, maduran antes, lo que les permite asegurarse el acceso a los machos y canibalizar machos indiscriminadamente sin tener un riesgo demasiado elevado de limitación espermática, que se sugiere porque en una muestra de 6 hembras, el tiempo de maduración explica el acceso a los machos (Fernández-Montraveta & Cuadrado, 2003), mientras que en un estudio con un tamaño de muestra más generoso pero sólo con hembras de maduración tardía, se muestra que el acceso a los machos baja enormemente a medida que progresa la estación de apareamiento (Moya-Laraño et al., 2003a). Por el contrario, las hembras "MFCL" son menos voraces y con menores tasas de ingesta, por lo que maduran más tarde. Estas hembras dóciles tienden a ser menos agresivas hacia los machos y primero copulan, obteniendo así un beneficio adaptativo al remediar la potencial falta de fecundidad. De hecho, probablemente dichas hembras tengan un menor acceso a los machos debido a que maduran más tarde y a que la densidad de machos disminuye a lo largo de la estación reproductora, probablemente por la depredación y el canibalismo de las hembras de maduración temprana ("SPOV") (Moya-Laraño et al., 2003a,b). En estas hembras, de forma paralela al aumento en la tendencia al canibalismo tras la cópula se produce un cambio significativo en la tasa de ingesta de alimento que lleva a tasas de engorde más altas con respecto a las hembras "SPOV", y favorece el acortamiento en el tiempo necesario para hacer la puesta. Este cambio en la voracidad alimenticia tras haber copulado permitiría a las hembras "MFCL" compensar el desarrollo tardío y las bajas tasas de ingesta pre-cópula, que pueden haber impuesto un coste adicional, ya que las hembras llegan a perder peso en esta fase. En las hembras "SPOV" por otra parte, no hay un cambio en la voracidad de forrajeo ni en la tendencia caníbal, es decir, los niveles de agresión se mantienen a lo largo de la estación reproductora lo que, junto a los resultados del manuscrito II, corrobora la existencia de un síndrome "spillover" en el comportamiento caníbal de las hembras "SPOV".

¿Cómo interaccionan las dos estrategias? ¿Son estrategias evolutivamente estables? El modelo (manuscrito IV) muestra que las estrategias "SPOV" Y "MFCL" pueden coexistir en una población bajo determinadas circunstancias ecológicas por selección dependiente de la frecuencia (Fisher, 1930). Las hembras más agresivas "SPOV" de maduración temprana pueden invadir poblaciones de hembras dóciles "MFCL", mientras que las hembras "SPOV" con tiempos de maduración idénticos a las "MFCL" son incapaces de hacerlo, por lo que la fijación genética de cada estrategia en la población depende fuertemente del tiempo de maduración. La estabilidad evolutiva de cada estrategia dependerá por tanto de las frecuencias relativas entre los fenotipos "SPOV" y "MFCL", así como por la eficacia biológica relativa. Así, para que una estrategia agresiva sea evolutivamente estable, el balance neto de costes y beneficios del canibalismo indiscriminado debe ser superior al de cualquier otra estrategia alternativa (Maynard Smith, 1978). El éxito de cada estrategia, además, depende de la naturaleza del ambiente en un año concreto y de la interacción entre factores genéticos y ecológicos. Las dos estrategias pueden competir y llegar en algunos casos a superar una a la otra dependiendo de factores como la disponibilidad de machos y de presas (en condiciones naturales) y la tasa de encuentros macho-hembra. Si, por ejemplo, la disponibilidad de machos es baja, las hembras "MFCL" serán favorecidas al asegurarse la fecundación de sus huevos, pero si es muy alta una estrategia "SPOV" probablemente sea más adecuada al maximizar la eficacia biológica de la hembra. Sin embargo, se puede predecir que una estrategia "SPOV" no evolucionará si las hembras sufren fuerte limitación espermática (baja densidad o movilidad de machos), ya que la probabilidad de producir un saco de huevos es relativamente baja con respecto a las hembras dóciles. Un aspecto interesante es que nuestros resultados empíricos (no anticipados en el modelo) muestran un coste asociado a una estrategia "MFCL" (pérdida de peso antes de la cópula) que podría aumentar el intervalo de tolerancia entre las dos estrategias, favoreciendo su coexistencia y persistencia evolutiva en poblaciones. Recientemente, se ha sugerido que los polimorfismos conductuales podrían mantenerse por selección negativa dependiente de la frecuencia (Wolf et al., 2007; Wolf & Weissing, 2010), de modo que una población debería evolucionar hacia un estado de equilibrio en el que los distintos tipos conductuales tuvieran las mismas garantías de fecundidad

(Maynard Smith, 1982). En el caso de las estrategias SPOV y MFCL, es más probable que ambas coexistan establemente cuando las bajas frecuencias de una estrategia afecten positivamente la eficacia biológica de las hembras de dicha estrategia. Este proceso de coexistencia dependiente de la frecuencia puede ser similar al que predice un modelo reciente que explica los procesos de invasión de especies en base a la existencia de distintos tipos conductuales en cuanto a sus niveles de agresividad, actividad y sociabilidad (Fogarty et al., 2011).

Los resultados del manuscrito II muestran también que las hembras dóciles (MFCL) pueden ejercer fuertes presiones selectivas sobre los rasgos fenotípicos de los machos, ya que tienden a atacar a los machos en peor condición y a copular con los de mejor condición, lo que contribuirá a generar variabilidad en el éxito reproductor masculino. Por el contrario, las presiones selectivas ejercidas por las hembras más agresivas deben ser relativamente más débiles, por lo menos en los rasgos que no tienen que ver con el comportamiento anti-depredador, dado que éstas no distinguen a los machos como fuente de esperma o alimento y los atacan indiscriminadamente, incluso independientemente del fenotipo del macho. Estos dos resultados son consistentes con la hipótesis de la elección de pareja (Elgar & Nash, 1988), según la cual el canibalismo sexual pre-copula sirve para descartar a los machos de peor calidad y aparearse con los de mayor calidad. Además, evidencian por primera vez que las hembras de diferente fenotipo conductual (personalidad) pueden actuar como agentes selectivos diferenciales sobre los fenotipos del macho a través del canibalismo sexual, lo que podría tener importantes implicaciones en el mantenimiento de la variabilidad genética de los machos.

Un resultado en apariencia contradictorio es que las hembras dóciles preferían copular con machos de mejor condición pero no de mayor tamaño corporal. Para que las hembras puedan seleccionar a los machos según su condición corporal, éste debería ser un rasgo fácilmente identificable por la hembra y cualitativamente relacionado con la eficacia biológica o la calidad genética del macho. Un estudio de campo con *L. hispanica* mostró que la condición corporal del macho es un rasgo altamente repetible a lo largo de la temporada reproductora, y que por tanto podría tener una base genética y estar asociado con

diversos rasgos que determinan la eficacia biológica del macho (Corcobado, 2011). Por ejemplo, los machos en mejor condición corporal tienen mayor movilidad en los contextos anti depredador y de búsqueda de pareja, lo que influirá positivamente en su éxito en el emparejamiento (Corcobado, 2011). Las hembras de *Hygrolycosa rubrofasciata,* una especie de la misma familia que *L. hispanica*, pueden seleccionar machos con mejor función inmune, ya que éstos suelen tener mayor movilidad y, por tanto, mayor probabilidad de ser encontrados por las hembras (Ahtiainen et al., 2004). De este modo, las hembras podrían discernir la calidad de los machos en base a su condición si ésta fuera una señal honesta de su superior calidad genética (Zahavi, 1975), obteniendo beneficios genéticos indirectos a través de la producción de descendencia de mayor calidad emparentada con estos machos. Por ejemplo, en la araña lobo *Pardosa milvina*, la tasa de cortejo del macho es un rasgo repetible dependiente de la condición y asociado con el éxito en el apareamiento, que podrían usar las hembras como indicador honesto de la calidad de sus parejas, ya que las hembras que se aparean con machos cuya intensidad de cortejo es mayor incrementan significativamente su fecundidad (Hoefler et al., 2009). Igualmente, en *H. rubrofasciata*, la frecuencia de tamborileo del macho, un componente importante del cortejo, es un indicador del estado inmunológico y de la viabilidad del macho que puede ser usado por las hembras para elegir a los machos con mejor capacidad inmunocompetente (Ahtiainen et al., 2001, 2004). Sin embargo, este comportamiento implica unos costes que son dependientes de la condición del macho (Kotiaho, 2000; Mappes et al., 1996). Los costes de mantener un cierto nivel de función inmune pueden ser relativamente bajos en individuos en mejor condición, al disponer de más recursos para invertir en la función inmune (Møller et al., 1998). Esto significa que la expresión de caracteres sexuales puede ser dependiente de la condición, y que los individuos en mejor condición pueden estar más capacitados para sobrellevar los costes de producir caracteres sexuales de mayor tamaño (Kotiaho, 2001). Sin embargo, en artrópodos aún no se ha corroborado un patrón general entre la función inmune y la condición. Por ejemplo, en *H. rubrofasciata* los costes asociados al tamborileo de los machos son dependientes de la condición, pero se desconoce si la función inmune también lo es. En *L. hispanica*, los machos adultos podrían estar señalizando honestamente su condición corporal mediante las

manchas negras de su abdomen, que crecen cuando lo hace la condición (Moya-Laraño et al., 2003b; N. Melguizo-Ruíz et al. 2007; J. Moya-Laraño & R. Rabaneda-Bueno, datos no publicados), ya que estas manchas son fácilmente detectables por las hembras durante la cópula. Si las hembras distinguen a los machos en base a estas señales (correlación franjas abdominales-condición corporal), sería de esperar que los machos elegidos por las hembras menos agresivas tuvieran manchas más conspicuas y/o de mayor tamaño. En línea con lo anterior, sería interesante conocer si existe alguna relación entre las franjas abdominales de los machos de *L. hispanica* y su capacidad inmunológica. Si estas manchas son caracteres sexuales secundarios producidos por pigmentos melánicos, el tamaño de estas manchas sería un indicador de la capacidad inmunológica del macho que variaría dependiendo de la condición de éste (Rantala et al., 2000; Siva-Jothy, 2000; ver también Ahtiainen et al., 2005).

Hay que destacar que, aunque los resultados obtenidos en esta tesis muestran que el canibalismo sexual es un comportamiento principalmente pre-cópula en *L. hispanica,* las hembras pudieron no estar exentas de costes si los ataques comprometieron los potenciales beneficios del emparejamiento con machos adicionales (poliandria). Por ejemplo, las hembras pueden necesitar el esperma de varios machos para fertilizar todos los huevos dentro del saco, lo que será determinante en el número de huevos viables y por tanto en su fecundidad (Elgar, 1992; Wise & Wagner, 1992). Las hembras de *L. hispanica,* en particular, producen sacos con proporciones variables de huevos fecundados y no fecundados (Moya-Laraño, 1999). Los machos pueden ser por tanto recursos limitantes para las hembra si éstas, tras aparease, tienden a atacar a todos los machos que encuentran. Datos no presentados del experimento 1 en manuscrito I muestran que hubo una relación negativa entre la proporción de huevos sin fecundar y el número de cópulas en que se vio involucrada una hembra, sugiriendo que las hembras pueden tener limitación espermática, especialmente si matan a todas sus potenciales parejas (J. Moya-Laraño, R. Rabaneda-Bueno, C. Fernández-Montraveta & M. Rodríguez-Gironés, datos no publicados). En este sentido, la poliandria proporcionaría a las hembras una fuente adicional de esperma para lograr una completa fertilización de los huevos. Alternativamente, esto podría significar que la

variabilidad genética conseguida aumenta la viabilidad de los huevos y su probabilidad de eclosión (e.g. Fedorka & Mousseau, 2002). Sin embargo, los datos del manuscrito III muestran que las hembras poliándricas no produjeron un mayor número de arañitas que las monándricas (datos no presentados en el manuscrito), lo que hace menos plausible esta hipótesis, y contrasta con los estudios realizados en invertebrados (McLeod & Marshall, 2009) y otros taxones inferiores (Marshall & Evans, 2007) que muestran un mayor éxito de fertilización de las puestas procedentes de hembras poliándricas respecto a las hembras monándricas. No obstante, la tendencia al re-emparejamiento de las hembras de *L. hispanica* puede ser decisiva para determinar si existe un "trade-off" entre el número de cópulas y el canibalismo. Por ejemplo, en este estudio las hembras mostraron variación en el grado de poliandria, que fue independiente del acceso que tuvieron a los machos, por lo que algunas hembras tendían a copular con un solo macho (monandria voluntaria) aun disponiendo de varias oportunidades para copular (manuscrito III).

El canibalismo sexual pre-cópula también pudo imponer un coste adicional si un alto grado de poliandria implica una mayor variación en los fenotipos de las arañitas (tamaño) que incrementa las probabilidades de supervivencia de la descendencia bajo condiciones ecológicas variables o impredecibles (hipótesis "bet-hedging", Slatkin, 1974; Watson, 1991, 1998). Los resultados del experimento de crecimiento de las crías en el laboratorio muestran que la descendencia procedente de madres que se habían emparejado con más machos tenían tamaños y tasas de crecimiento más variables que las hembras que sólo copularon con un macho (manuscrito III). Sin embargo, cuando se enfrentó a la progenie de madres poliándricas a un ambiente heterogéneo en cuanto a la cantidad de alimento, las arañitas de madres poliándricas no tuvieron un mayor éxito ni en la supervivencia ni en el crecimiento, indicando que la variabilidad inducida por la poliandria no tuvo ningún efecto. Aunque estos resultados no son consistentes con la hipótesis del "bet-hedging", los efectos sobre la variabilidad de tamaños podrían requerir el seguimiento de la progenie a lo largo de varias generaciones para que empezaran a ser detectables en una población, tal y como predice esta hipótesis. Además, podría ser que el rango de ambientes simulado en nuestro experimento de laboratorio no

reflejara exactamente las presiones de selección a las que están expuestas las arañitas durante la dispersión.

El papel de los machos en las interacciones caníbales puede ser importante para entender los resultados discutidos hasta el momento. Aunque en esta tesis no se evaluaron los costes y beneficios del canibalismo sexual sobre la eficacia biológica de los machos, éstos son más o menos patentes por el hecho de que en casi la totalidad de los ataques el macho no se había apareado antes con la hembra, lo que significa que el beneficio del canibalismo sexual para la mayoría de los machos canibalizados fue cero. Por otro lado, los costes del canibalismo sexual pre-cópula pudieron variar entre los machos dependiendo de la probabilidad de encontrar una hembra del tipo "SPOV" o del tipo "MFCL" y de la época dentro de la estación de apareamiento. En general, estos costes sobre los machos derivan de la falta de paternidad en el encuentro con la hembra caníbal o la reducción de las posibilidades de emparejamiento futuro, que están relacionados uno con el otro (Bateman, 1948).

Por último, el comportamiento caníbal de las hembras debería imponer una fuerte presión selectiva sobre los machos que promovería la evolución de contra-adaptaciones que evitaran los ataques de las hembras. Los estudios con *L. hispanica* sugieren que los machos no se aproximan aleatoriamente a las hembras, y hasta cierto punto son capaces de evitar el canibalismo (Moya-Laraño et al., 2003a; Moya-Laraño et al., 2004). Por ejemplo, los machos pueden acercarse a las hembras pequeñas y en mejor condición, porque podrían ser menos voraces y el riesgo de ser canibalizado menor (Moya-Laraño et al., 2003a). Un resultado del experimento de campo 2 (manuscrito II) que se suma a esta evidencia muestra que los machos tendían a permanecer inmóviles al exponerse a las hembras más voraces, por lo que de algún modo eran capaces de reconocer a estas hembras agresivas. Sin embargo, debido a que ni el tamaño ni la condición explicaron la agresividad de la hembra, es posible que los machos utilizaran otras pistas para evaluar el riesgo de aproximarse a una hembra agresiva, independientemente de que fueran de mayor tamaño. Sería interesante investigar si los machos son capaces de explotar pistas en las hembras que indiquen una mayor agresividad, de modo que puedan reconocer a estas hembras y evaluar así el riesgo potencial de

cortejarlas. Aunque en el experimento del manuscrito II los machos no tuvieron la oportunidad de decidir a qué hembras acercarse, la reacción de paralizarse ante una hembra agresiva puede ser una aproximación de las preferencias de los machos por determinadas hembras cuando se desplazan en busca de pareja, la cual podría ser explorada en futuros estudios.

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CONCLUSIONES

Conclusiones

1. En poblaciones naturales de la tarántula ibérica (*Lycosa hispanica*) el canibalismo sexual pre-cópula es un comportamiento frecuente, que tiende a aumentar significativamente con la disponibilidad de machos.

2. El canibalismo sexual pre-cópula es principalmente un comportamiento de forrajeo adaptativo. El consumo de un macho sirve para paliar la limitación nutricional y mejorar la fecundidad de la hembra. La mayoría de hembras se comporta adaptativamente atacando a los machos una vez que se han asegurado el esperma para fertilizar sus huevos, evitando con ello la falta de fecundación.

3. En algunas hembras el canibalismo sexual es un comportamiento subóptimo, producto de la alta voracidad alimenticia de las hembras que depende de su "personalidad" agresiva. Estas hembras tienden a canibalizar machos indiscriminadamente, aunque no se hayan apareado antes.

4. Las altas tasas de ingesta de alimento implican madurar antes, lo que probablemente permita a las hembras más agresivas eludir los costes de los altos niveles de limitación espermática al final de la estación reproductora. Las hembras menos voraces (tipo dócil), que se alimentan menos y son menos agresivas hacia los machos antes de aparearse, maduran más tarde y pueden tener un riesgo por limitación espermática. Sin embargo, los costes pueden no ser demasiado altos, ya que estas hembras tienden a copular primero para asegurarse el esperma que fertilice sus huevos, y aumentan su tasa de ingesta de alimento tras haberse apareado, lo que les permitiría compensar las pérdidas de peso sufridas durante el período pre-copula.

5. Las observaciones *in situ* de hembras dóciles y agresivas (personalidades agresivas), asociadas a dos estrategias distintas (SPOV *vs.* MFCL) sugieren la existencia de polimorfismos conductuales por equilibrio dependiente de la frecuencia, tal y como predice el modelo Ungoliant.

6. La personalidad de la hembra influye en los procesos de elección de pareja y en el canibalismo sexual, lo que puede contribuir a generar variabilidad en los niveles de selección sexual sobre los machos. Esto podría ayudar a explicar el mantenimiento de una alta variabilidad de fenotipos masculinos en la naturaleza a pesar de las fuertes presiones selectivas que tienden a actuar en contra.

7. En consonancia con la hipótesis de "bet-hedging", la poliandria está asociada a crías con mayor variación tanto en tamaños al nacer como en tasas de crecimiento. Sin embargo, no se encontró que la poliandria aumentara el éxito reproductivo de las hembras en ambientes heterogéneos, probablemente porque nuestro experimento no capturó la heterogeneidad ambiental natural.

Conclusions

1. In natural populations of the Iberian tarantula (*Lycosa hispanica*) pre-copulatory sexual cannibalism is a common behavior that tends to increase significantly with male availability.

2. Pre-copulatory sexual cannibalism can mainly be interpreted as an adaptive foraging behavior of females. The consumption of a male may serve as a form to redress nutritional unbalances and to improve female fecundity. A high proportion of females behave adaptively by attacking males once they have ensured sperm to fertilize their eggs, thereby preventing the lack of fertilization.

3. In some females, pre-copulatory sexual cannibalism is a suboptimal behavior, resulting from the high levels of female foraging voracity which is related to an aggressive personality. These females tend to cannibalize males indiscriminately, even if they are still unmated.

4. High rates of food intake imply earlier maturation, which would probably allow the most aggressive females to avoid the high costs of sperm limitation at the end of the mating season, by accessing to a higher number of males earlier in the season. The less voracious females (docile type), which feed at a low rate and do not tend to attack males before mating, are likely late-maturing females that have a risk of sperm limitation. However, costs may not be too high since these females mate first to ensure sperm for egg fertilization, and then increase their food intake to higher rates than the aggressive females, which may likely allow the former to outweigh the mass losses incurred during the pre-mating period.

5. The *in situ* observations of both docile and aggressive females (aggressive personalities) which are associated with two different strategies (SPOV *vs.* MFCL) suggest the existence of behavioral polymorphisms by frequent-dependent equilibria, as predicted by the model Ungoliant.

6. Female personalities influence sexual cannibalism and mate choice processes and thus could potentially promote variability in the levels of sexual selection on male phenotypes. This could help explain the persistence of male phenotypes which are highly variable in nature albeit the strong selective pressures acting against some male phenotypes.

7. In line with the bet-hedging hypothesis, polyandry is associated with high variability in growth rates and the hatching size of progeny. However, polyandry did not increase female fitness in heterogeneous environments, probably because our experiment did not capture the natural range of environmental heterogeneity.

AGRADECIMIENTOS

Agradecimientos

Nunca antes estuve sentado tanto tiempo frente al tablero del mundo, el que se ve a través del propio yo, en una interminable y rocosa partida en la que parecía estar en juego mi propio destino. Si el caos declina la balanza hacia un lado u otro de la vida, en esta partida la vida renace a partir del propio caos. Como el ave Fénix, a partir de las propias cenizas del desconcierto, eludiendo la propia vida para reencontrarse con ella. Ahora que esta tesis es ya una realidad, me gustaría agradecer a todas aquellas personas que han hecho posible el momento de escribir estas primeras líneas, quizás algo abstractas, y por primera vez en esta memoria, sin concesión alguna a la lógica científica.

En primer lugar, quisiera agradecer a mis directores de Tesis. Al Dr. Jordi Moya Laraño, por depositar su confianza en mí y ofrecerme la oportunidad de formarme como científico. Qué lejos queda ya el día en que nos conocimos en Aguadulce, cuando me hablaste por primera vez de tus arañas y de los proyectos que tenías en mente. Gracias por proporcionarme los medios a tu alcance para el desarrollo de esta tesis, por los numerosos conocimientos que me has transmitido a lo largo de estos años, y por ofrecerme la formación profesional necesaria para abrirme paso en este incierto mundo de la investigación básica. A la Dra. Carmen Fernández Montraveta, que me acogió durante dos largas temporadas en su laboratorio de la Facultad de Psicología de la UAM, por su tiempo y paciencia durante interminables jornadas para llevar a buen puerto los experimentos, y por tus consejos y ánimos en esta última etapa que han sido muy importantes para concluir esta tesis.

También quiero agradecer a Miguel A. Rodríguez Gironés y a David H. Wise por la inestimable ayuda que me prestaron durante algunas fases de esta tesis. A Nieves y a Eva de Mas, la fotógrafa oficial y partícipe de los experimentos, que hicieron más llevaderas las intensas jornadas en el campo.

A Gregorio Moreno Rueda, con quien coincidí durante mi etapa en el Departamento de Biología Animal y Ecología de la Universidad de Granada, por la pasión que siempre transmites en lo que haces, y por haberme animado a realizar

estudios de doctorado y contar conmigo cuando me encontraba en un período de horas bajas.

A Begoña Peco, mi tutora de los cursos de doctorado, por estar siempre dispuesta a ayudarme en lo que fuera durante la realización del DEA, y mantener un trato cálido y amable a través del tiempo.

Al Museo Nacional de Ciencias Naturales de Madrid por todas las facilidades que nos dieron para desarrollar experimentos en su laboratorio.

A mis compañeros becarios de la EEZA, muchos de los cuales empezaron a la vez que yo y forman ya parte de la historia "chumberil". A Miguel, Ana, Joao, Iván, las dos Lauras, Oriol, Belén, Lupe, Sebas, Beatriz,…con quienes tuve la oportunidad de compartir buena parte de esta incierta etapa, desde nuestros inicios en esto de hacer una tesis. Por los buenos momentos que pasamos, el buen humor y compañía, gracias de corazón. A todas los profesionales de la EEZA, investigadores y personal de las distintas áreas, que siempre tuvieron una palabra de aliento; a personas como Andrés Castro, Juan Leiva, Paco Valera, Paquita, Mª Luisa u Olga Delgado, grandes personas que hacen que todo sea más fácil.

A Virginia, Sara, Nere y David, con quienes pasé largas temporadas en el campo y en el laboratorio en Madrid y Almería, y fueron una ayuda importante en el desarrollo de los experimentos. Quiero agradecer también a Alejandro, Alfredo, Tomás y Manolo, por su importante apoyo logístico y por estar siempre dispuestos a echar una mano.

Mi más sincera gratitud hacia el Dr. Alejandro Córdoba Aguilar, con quien tuve la fortuna de trabajar durante mi estancia en México, abriéndome las puertas de su casa desde el principio. Por acogerme en su laboratorio en el Instituto de Ecología de la UNAM, y por darme la oportunidad de asomarme al apasionante mundo de la inmunología de invertebrados. Tampoco puedo olvidarme de Jorge Contreras, "el alma de la fiesta" del mismo grupo de investigación, y un gran profesional. Por los grandes momentos que pasamos durante los trabajos de campo y laboratorio y por descubrirme sitios increíbles de la geografía azteca a bordo de aquella preciosa Chevrolet blanca. Y cómo no, por hacerme partícipe de la famosa celebración del Día de Muertos.

A la buena gente de Xiapas, a las que tuve el placer de conocer en Veracruz, por su humildad y generosidad, y por entregarse al máximo desde el primer día, invitándome a visitar su tierra siempre que quisiera.

Quiero agradecer especialmente a Haydeé, la primera persona que conocí nada más aterrizar en México D.F., quien desde entonces no se separaría de mí hasta mi partida. Por convertir mi estancia en momentos maravillosos e inolvidables en los que me sentí como en casa, enseñándome los sitios más recónditos de esa gran urbe, y por esas veladas siempre acompañadas de una deliciosa Caguama. Gracias por ser más que una compañera de trabajo con la que forjaría una relación de amistad de esas de larga duración.

A mis amigos, con mención especial al trío calavera, Juanra, Miguel "lobo" y Charlie por tener que aguantarme y haber sido partícipes de todo esto, y por haber estado siempre presentes en esta etapa de alegrías y penurias. También a Pablo, Luis, Ana, Jesús, Antonio....a Mar por renovar mis esperanzas en esta última etapa, y a Sigi y Andrea que estuvieron a mi lado durante uno de los momentos más delicados de mi vida, nunca os olvidaré. A Fran, por descubrirme la belleza natural que aguarda en los sitios más recónditos de la provincia de Almería, y por todos los buenos momentos que pasamos recorriéndola de arriba abajo.

No puedo olvidarme de aquellos que son siempre una fuente de inspiración que me empuja a salir adelante en los peores momentos y me impulsan a mejorar día a día. A la memoria de David, Rebeca y Lorenzo, tres grandes amigos que ya no están aquí pero que siempre llevaré en mis recuerdos y en mi corazón.

A mi familia, a mi abuela Ramona, y a mis abuelos Pedro y Paqui que ya no están entre nosotros, pero a los que jamás olvidaré. A mis tíos Alberto, Andrés y Pedro, a mis tías Jose y Juani, a mis primos Alberto y Pedro, y a mis primas Miriam y Olivia, por las palabras de cariño que tan importantes fueron en momentos clave y por poder contar siempre con vosotros. También a Lourdes, Ana, Andrew y Manolo, a mis primas Marta y Sonia y al resto de familiares, tíos y primos por su apoyo y ánimos.

Y por último, a las personas que más quiero:

A mis hermanos Juanjo, Raúl y Javier, por proporcionarme el aliento y apoyo cuando más los necesitaba, por estimularme para que no bajara los brazos cuando todo parecía perdido y por creer siempre en mí y no permitir que yo dejara de hacerlo. Gracias por tenderme la mano a lo largo de estos interminables años y por vuestro apoyo incontestable. El origen de todo esto y de mi propia existencia, mis padres Juan José y María del Carmen, a los que quiero dedicar esta memoria, por vuestra infinita comprensión y generosidad ilimitada, y por ser el pilar fundamental en todo lo que soy. Por vuestro apoyo incondicional no sólo durante esta etapa de mi vida sino durante todos los momentos que me han llevado hasta este preciso instante, por vuestra dedicación y educación constantes siempre pensando en lo mejor para mí. Por recordarme que nada es imposible, motivándome con vuestro ejemplo a superar todas las adversidades que iban apareciendo en el camino. Por infundirme ya desde muy pequeño el amor por la naturaleza, el valor del esfuerzo y la perseverancia, y la importancia de no rendirse nunca a pesar de todas los obstáculos que pudieran aparecer en el camino. Por todo ello, no tengo palabras para expresar lo afortunado que soy por teneros.

De donde vengo, al otro lado del charco, y en otro continente, al menos antes existían parajes naturales bellos y únicos como el monte Gurugú o los pinos de Rostrogordo, entrando ya en territorio marroquí, en los que tuve la fortuna de aventurarme durante mi juventud. Si de niño se es dueño de las sensaciones, hoy puedo decir que en ningún otro lugar de ese pequeño cónclave del territorio español que es Melilla, quedaba tan reducida la percepción de tiempo y espacio a tan simples conceptos. Explorar aquellos lugares era como vencer al tiempo, y olvidar que el espacio se abría más allá de los "muros" de la ciudad. Esos lugares se convirtieron en santuarios, y más tarde formarían ya una parte importante en el devenir de mi existencia, al despertar en mí un gran respeto y amor por la naturaleza, siempre reforzados por la educación que recibí. Pero afortunadamente pude ver que aún había una inmensidad por descubrir más allá, durante los maravillosos viajes con mi familia, recorriendo los sitios más hermosos de la geografía española, y que guardo ahora como un tesoro en forma de recuerdos a los que acudir. Con anhelo veo pasar las imágenes que a veces me proporcionan esos recuerdos, para darme cuenta de

cómo ha cambiado todo en un tiempo tan relativamente corto, y para tomar conciencia del imponente valor no ya del propio tiempo, sino de lo vivido durante el transcurso del mismo. Aunque ninguna palabra puede compensar el sinsabor del tiempo pasado, sí puede aliviar el dolor de lo que está por partir. Por ello y por el tiempo que debo a cada uno de los que estuvieron conmigo en los momentos difíciles, gracias a todos.

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